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PALAEONTOLOGY

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THE SEQUENCE OF GRAPTOLITE FAUNAS

by O. M. B. BULMAN

Annual Address for 1957, delivered 12 March 1958

INTRODUCTION

It was Lapworth's *Geological Distribution of the Rhabdophora* (1880) that finally established the stratigraphical value of the graptolites, but any general discussion of the succession of graptolite faunas may take as its starting-point *The Graptolite Faunas of the British Isles*, published by Miss Elles in 1922. In this, she expresses the evolutionary and philosophical conclusions reached after more than twenty years' work in collaboration with Lapworth and Miss Wood in the preparation of the famous *Monograph* (Lapworth, Elles, and Wood 1901–19). The evolutionary history of the entire group was analysed in terms of certain general trends—stipe reduction, change in direction of growth, and various trends in thecal elaboration—and stress was laid on their stratigraphical significance. The faunal section was, above all, designed to enable the stratigrapher to obtain a relatively close approximation to the age of a representative graptolite assemblage by assessing its general faunal characters, without resort to extensive specific identification. Four main faunas were recognized, and with their subfaunas have become the accepted standard; these are listed below with their original definitions:

MONOGRAPTID FAUNA

The fourth graptolite fauna is characterized pre-eminently by the enormous development of the uniserial scandent graptolites the *Monograpti*.

5. Predominance of *Monograpti* with simple thecae of the *Dichograptus* type. (Lower Ludlow zones.)
4. Acme and waning of hooked *Monograpti*. Acme of *Cyrtograpti*. (Wenlock zones.)
3. Predominance of *Monograpti* of hooked type. Acme and extinction of isolate type. Waning of lobate type. (*M. sedgwicki* to *M. crenulatus*.)
2. Predominance of *Monograpti* of isolate and lobate types. Waning of *Diplograptidae*. (*M. gregarius* to *M. convolutus*.)
1. Predominance of *Monograpti* of exclusively 'old-fashioned' types. Numerous *Orthograpti* and *Climacograpti*. (*O. vesiculosus* to *M. cyphus*.)

DIPLOGRAPTID FAUNA

The most noteworthy and characteristic feature about this third fauna is the profusion of *Diplograpti* of the *Orthograptus* type.

3. Presence of abundant *Orthograpti* with *Climacograpti* and large *Glyptograpti*. Absence of *Dicellograpti*. (*A. acuminatus* to *G. persculptus*.)
2. Presence of *Orthograpti* with *Dicellograpti* and *Climacograpti* of simple thecal type.
(*D. complanatus* to *D. anceps*.)
1. Acme of large *Orthograpti*. Persistence of *Dicellograpti* and *Dicranograpti* of complex thecal type. (*C. wilsoni* to *P. linearis*).

[Palaeontology, Vol. 1, Part 3, 1958, pp. 159–73.]

LEPTOGRAPTID FAUNA

Characterized by a new element, that of elaboration of the thecal type, the older lines of evolution being temporarily arrested with the attainment of the reclined (*Leptograptus* and *Dicellograptus*) or scandent (*Glyptograptus*) position.

2. Presence of graptolites characterized by simple sigmoid thecae together with complex types. Scandent biserial forms increasingly abundant. (*M. multidens* and *C. peltifer*.)
1. Acme of graptolites characterized by simple sigmoid thecae (absence of complex types). Reclined uniserial forms together with scandent biserial forms. (*G. teretiusculus* to *N. gracilis*.)

DICHOGRAPTID FAUNA

All the earliest Graptolites are branched forms, possess simple thecae, and develop according to the *Dichograptus* plan, whilst the lines of evolution that can be traced in them are those of:

(*a*) simplification in branching,
(*b*) change in direction of growth (pendent to scandent).

- Two-branched forms
  - *b.* Pendent series (*D. bifidus*–*D. murchisoni*).
  - *a.* Horizontal series (*D. extensus*–*D. hirundo*).
- Many-branched forms becoming simpler
  - *b.* U. *Dichograptus* zone (presence of horizontal *Tetragrapti*).
  - *a.* L. *Dichograptus* zone (rarity of *Tetragraptus*).

The scheme as a whole has justified the claims of its author. Contrary perhaps to popular belief, many graptolite zones have a restricted geographical distribution, as is only too apparent to those who attempt the correlation of graptolitic successions; and it is possible to define faunal units which are considerably bigger than zones, but which can be applied over wider areas, are more easily identified (on general characters), and also to the palaeontologist present an epitome of the geological history of the group. Discoveries of the past thirty years, however, while confirming some of the characteristics Dr. Elles employed for this purpose, have raised doubts as to the value of others. For example, it was not long before Dixon (1931) questioned the reliability of the Dichograptid faunal subdivisions, and more recently, Harris and Thomas (1940*a* and *b*) have challenged the assumed phyletic basis of the stipe-reduction series.

Criticisms such as these could be met by comparatively minor modifications, but more serious difficulties have arisen in connexion with the Leptograptid Fauna. In a recent review, Harris and Thomas (1956) have remarked that to put the Leptograptid Fauna stratigraphically below the Diplograptid Fauna 'is not warranted by observed facts' and, in effect, that we in Britain seem to have got the Leptograptid and Diplograptid Faunas inverted. To this it may be replied that they are themselves misinterpreting the basis of Elles's Leptograptid and Diplograptid Faunas. The Leptograptid Fauna was defined to include as essential components diplograptids, *Dicellograptus*, and *Dicranograptus* as well as leptograptids, united by the prevalence of some more highly modified type of theca; and the Diplograptid Fauna was largely based on the prevalence of *Orthograptus*. But it may well be felt that a terminology which admits such an interpretation is misleading. Moreover, revised correlation of graptolitic and non-graptolitic representatives of the Llandeilo and basal Caradoc has introduced further complications, because the Leptograptid Fauna can hardly now be claimed to correspond to any precise stratigraphical unit. There would seem little purpose in attempting to define and isolate a fauna between these particular limits in the absence of some compelling morphological or evolutionary reason, and for that the Leptograptid Fauna is altogether too heterogeneous.

If this be admitted, then the necessary revision becomes a more extensive problem involving the Dichograptid, Leptograptid, and Diplograptid Faunas, and affords an opportunity to recast the whole faunal sequence. As a preliminary to this it will be helpful to review very briefly the salient features in the general evolution of the graptolites.

EVOLUTION OF THE GRAPTOLITES AND ITS BEARING ON FAUNAL DIVISIONS

The relations of the Graptoloidea to the Dendroidea are incomparably better understood than they were thirty years ago, and remarkably detailed morphological studies of both these Orders have been supplemented by faunal discoveries in the Tremadoc revealing a wide range of transitional genera. There can be no doubt that the earliest graptoloid family, the Dichograptidae, was polyphyletic, and that its separation from the dendroids was a gradual process of long duration. In fact, it is becoming clear that there exists an easily recognizable transitional fauna, dendroid as to structure but graptoloid in habit, antedating the main Dichograptid Fauna. It is a fauna that is only poorly represented in this country.

Within the Dichograptidae, the pattern of evolution is now recognized as being far more complex than was hitherto realized. While reduction in the number of stipes is undoubtedly a general trend, the stipe-reduction story has evidently been greatly oversimplified and various intermediate stages are not inevitably present. But it is sufficient for the present purpose to recall that, in rocks of Arenig age, members of this family entirely dominate the graptolite assemblage and necessitate the recognition of a Dichograptid Fauna.

Along whatever lines it may have been evolved, the two-stiped dichograptid *Didymograptus* represents a relatively stable form, and to judge from the number of species, it is the most important genus of the family. From it have presumably descended the leptograptids, dicellograptids, and dicranograptids which form such a distinctive element of Middle and Upper Ordovician faunas. Details of their descent are lacking, but it is not unreasonable to regard them as a steady differentiation and radiation of late dichograptid stock. That is to say, there is stratigraphical support for the morphological evidence linking leptograptids and dicellograptids to dichograptids and anisograptids in a continuous evolutionary series.

The origin of scandent forms, biserial and uniserial, is on the contrary disconcertingly obscure and abrupt. It is unnecessary here to discuss vague theories as to their origin (Bulman 1947, p. x and 1954*a*), but it is relevant to admit that we no longer attach any special significance to *Dicellograptus* and *Dicranograptus* as intermediate stages in the evolution of biserial forms, and that there are even difficulties in the way of accepting *Dimorphograptus* as a direct ancestor of *Monograptus*. Yet the very abruptness of their origin, and their novelty in rhabdosome design, makes these scandent forms the more significant in the general succession of graptolite faunas. Moreover, it has been shown that the cryptograptids are so different in structure and development from the true diplograptids as to necessitate a completely separate origin, and the fact that they were almost contemporaneous only reinforces the importance of biserial forms in the faunal succession.

Now the first appearance and exuberant spread of *Monograptus* is already recognized in the existing faunal scheme; but its curiously exact parallel, that of the biserial graptolites, is not, for it long antedates the base of Miss Elles's Diplograptid Fauna. Here surely is the feature we are seeking to replace the Leptograptid Fauna—an evolutionary event compared with which the deployment of the *Leptograpti* and *Dicellograpti* is of subfaunal importance.

To give effect to this proposal involves, as we shall find, not only expanding the former Diplograptid Fauna, but docking the tail of the Dichograptid Fauna. Consequently the revised scheme may, if adopted, create some initial confusion, for there seems no way to avoid using the same terms Dichograptid and Diplograptid Fauna with a different implication. But I believe the new faunas express as objectively as possible the known facts of morphology and stratigraphical distribution, and that they lose nothing of their value to the stratigrapher; indeed, attention has been drawn to the incoming of diplograptids as marking an important boundary in local successions by many authors before me.

Accepting the Monograptid Fauna unchanged, the four principal faunas here recognized are Anisograptid, Dichograptid, Diplograptid, and Monograptid, the last two being divided into four or five subfaunas.

1. THE ANISOGRAPTID FAUNA

The first widely distributed graptolite fauna is that of the Tremadocian comprising various epiplanktonic species of *Dictyonema* (such as *D. flabelliforme*) and their pendent and horizontal anisograptid descendants *Anisograptus*, *Clonograptus*, *Adelograptus*, *Bryograptus*, *Staurograptus*, &c. It is a transitional, but essentially a dendroid, fauna, and as such is sufficiently distinct from the Dichograptid Fauna of the Arenig to stand alone.

In north-west Europe, *Dictyonema flabelliforme* constitutes a well-recognized base to the fauna, with the varieties *sociale* and *parabola* predominating in the lowermost beds. *D. flabelliforme flabelliforme*[1] follows, associated with *Anisograptus* in Norway, and with *Clonograptus* and *Adelograptus* in Sweden and Britain. In the higher part of the fauna, these anisograptids tend to occur alone, or in association with *D. flabelliforme norvegicum* (Hede 1951; Bulman 1954*b*). There is a rather unexpectedly local character about many of these developments, and the correlations of their various zones and subzones cannot yet be considered firmly established. Tjernvik's revision of the *Dictyonema* Shales of south Sweden (now in the press) may help to clarify the position. Norway seems to have as much in common with the maritime provinces of North America as with other parts of Europe, and holds the key to transatlantic correlation. The lowest beds with *D. flabelliforme* alone are also known from Belgium (Lecompte 1948). Koliha (1926) reported *D. flabelliforme* and *Staurograptus* in Lower Tremadoc 'of Baltic type' from Břežany, Bohemia, but Prantl and Přibyl (1949) have questioned this correlation and from their published figures I do not regard it as proved that the Anisograptid Fauna occurs here at all. The well-known dendroid fauna described by Kozlowski (1948) from the Tremadocian of Poland is quite distinct from this epiplanktonic Anisograptid Fauna.

In North America, the Anisograptid Fauna is encountered in Cape Breton (Nova Scotia), Navy Island (New Brunswick), Newfoundland, along the southern shores of the St. Lawrence, and in New York State, whilst in the west, *Dictyonema flabelliforme* by itself has been recorded (Ruedemann 1930) from the Chushina Formation of British Columbia. The richest and best known of these assemblages is from the Matane Shales of Quebec, where *Anisograptus*, *Staurograptus*, and *Triograptus* are associated with species of siculate *Dictyonema* different from but perhaps related to *flabelliforme*, and with an early *Didymograptus*. The absence here of *D. flabelliforme* makes the exact correlation of the fauna rather uncertain, but it is probably lower Tremadoc (Bulman 1954*b*). The remaining faunas stand in need of revision, and records of *D. flabelliforme* cannot always be accepted at their face value; but at Green Point (Newfoundland) species of *Anisograptus* very close to those of Matane are associated with various *Dictyonema* species, one of which appears close to the Matane *canadense* while another seems at most varietally distinct from *flabelliforme*.[1] The implication would appear to be that there is no great disparity in age between the *D. flabelliforme* and *D. canadense* anisograptid faunas. As claimed by Hahn (1912), Matthew's *Clonograptus proximatus*, associated with '*D. flabelliforme*' in New Brunswick, is almost certainly *Staurograptus*, and *Clonograptus* is not known for certain to occur at all in the Tremadocian of the Eastern Provinces.

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[1] Obut (1953) has claimed that the type specimens of *D. flabelliforme* are identical with the variety that has since been called *norvegicum*, but there is some doubt about this and I am here retaining the name *flabelliforme* in its established usage.

Again, at Famatina and Santa Victoria, Argentina, there are several varieties of *Dictyonema flabelliforme* associated with *Anisograptus* species very close to those of Matane (Turner 1950).

All these occurrences appear to be separated from the Arenig by a considerable time interval, and the only undoubtedly Upper Tremadoc graptolites at present known are those of a small faunule described by Monsen (1925) from the *Ceratopyge* Shale near Oslo. This comprises *Triograptus*, some diminutive *Didymograptus* species, some rather fragmentary anisograptids (recorded as *Clonograptus* and *Bryograptus*, but almost certainly including *Anisograptus*), and a poorly preserved *Dictyonema*. Berry (1957 *in litt.*) has recorded *Clonograptus*, *Anisograptus*, and *Adelograptus*, again with a diminutive *Didymograptus*, from the base of the Marathon formation in Texas, which may prove to be an Upper Tremadoc fauna, and this is perhaps the only record of true *Clonograptus* from the Tremadoc of North America.

In Australia, the Anisograptid Fauna is evidently represented by the *Staurograptus* faunule (*Staurograptus* and two small species of siculate *Dictyonema*) of the basal Lancefieldian, La 1 (Harris and Keble 1928). This does not correlate readily with any of those mentioned above, but it is separated by over 1,000 feet of barren strata from the burst of *Clonograptus* and *Bryograptus* that characterizes La 2 (Harris and Thomas 1938) which may itself be Upper Tremadoc rather than lowermost Arenig. There is some evidence for the occurrence of an Anisograptid Fauna of more Atlantic type in New Zealand, where *Triograptus*, associated with various other anisograptid genera and with a *Didymograptus*, is reported by Benson and Keble (1935).

The records of *Dictyonema flabelliforme* from the Yehli formation in north China (Sun 1935), from Liaotung (Mu 1952), and from S. Chosen (Kobayashi and Kimura 1942) all appear to me doubtful, and they could well be Arenig species. Similarly, the fragmentary anisograptids figured by Mu (1955), associated with various *Dictyonema* and *Dendrograptus* species, are not very convincing; they have little in common with the true Tremadocian faunas noted above.

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[1] I am indebted to Professor Whittington for photographs and specimens of this material which is now being systematically collected and described.

The presence of small but apparently genuine *Didymograptus* species in the Anisograptid Fauna is of considerable interest in its bearing on dichograptid evolution. It also suggests that, when any considerable upper Anisograptid Fauna is discovered, true dichograptids may well be found to constitute a significant element in it, and the Anisograptid Fauna will be seen to merge gradually into the Dichograptid Fauna. Already it is known that the lowermost beds of the Arenig (other than in Britain) characteristically yield an abundance of *Clonograptus* and *Bryograptus*. It has never been proved that these Ordovician species possess bithecae and are in fact true dendroids, and if they do not they should logically be distinguished generically from their Tremadoc representatives; but this will hardly assist the stratigrapher in his general assessment of the fauna.

2. THE DICHOGRAPTID FAUNA

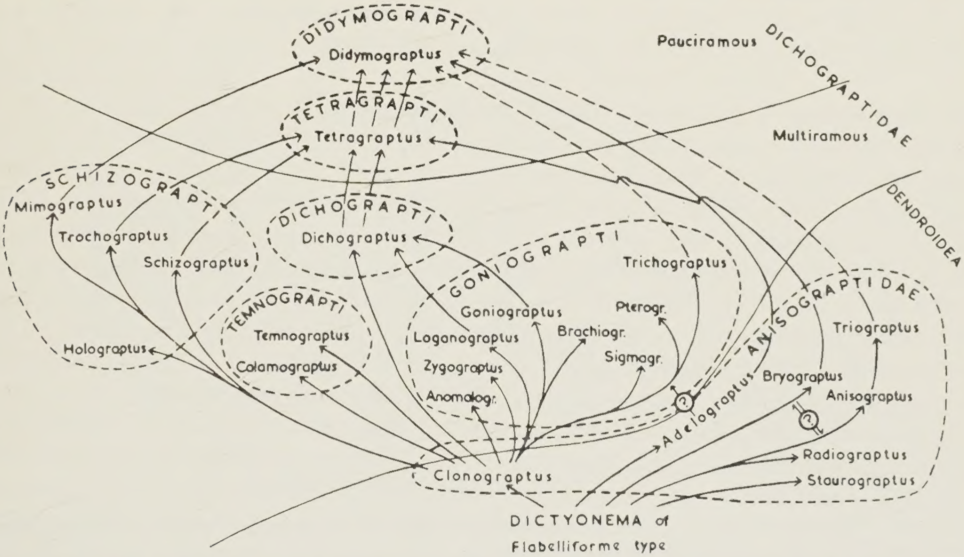
The generally accepted zoning of the Arenig in Britain is essentially that of Elles (1904), but owes much to the work of Marr (1894) on the Skiddaw Slates and is closely linked with the evolutionary concepts of Nicholson and Marr (1895). From the latter originated the idea that the two-stiped genus *Didymograptus* is a stage, independently attained from multiramous dichograptid ancestors by many different lines of descent through various *Dichograptus* and *Tetragraptus* species. The inference was that Arenig strata will show successive concentrations of *Dichograptus*, *Tetragraptus*, and *Didymograptus*. Elles (1922) qualified this by pointing out that the pendent series evolves more slowly than the horizontal series, but in the zonal scheme of the *Monograph* and in Elles (1922) a *Dichograptus* zone finds its place at the base, and in 1933 two horizontal *Tetragraptus* subzones were introduced between it and the *extensus* zone.

This faunal sequence was challenged by Dixon (1931), who found little stratigraphical evidence for such a precise transition in the Skiddaw Slates, claiming that many of the species concerned are long-ranged and that many-branched dichograptids are not necessarily indicative of a low stratigraphical horizon. Recently, in some still unpublished work, Jackson (1956) has again failed to find any stratigraphical support for the existence in the Skiddaw Slates of the *Dichograptus* and *Tetragraptus* zones, although he confirms the presence of the upper three *extensus*-subzones of Elles 1933. The *Dichograptus* zone has never been recorded elsewhere, and I think it must be agreed that there is no stratigraphical evidence for its existence. Nor does there seem strong evidence as yet for the occurrence of any marked concentration of *Tetragraptus* in the lower portion of the British Arenig.

Abroad, Harris and Thomas (1940*a* and *b*) criticized the theoretical concepts underlying this part of the faunal scheme, considering it improbable that *Loganograptus* is an intermediate between *Clonograptus* and *Dichograptus*. If I read them aright, they even doubt the close relation of *D. octobrachiatus* to any *Clonograptus* species, although accepting that some rare *Dichograptus* species with a long funicle and second-order stipes may logically be derived by stipe reduction from a *Clonograptus* ancestor. These authors further suggested that some *Tetragraptus* and *Didymograptus* species might well be derived from *Schizograptus* and *Trochograptus* ancestors, and regarded the table of dichograptid descent then current as greatly over-simplified. The possibility of direct derivation of *Didymograptus* species from Anisograptid ancestors has also been suggested (Bulman 1941, 1950*a*), and all these complications are incorporated in the tentative phylogenetic table, text-fig. 1.

Finally, as Dixon and others have observed, many of the common species such as *T. quadribrachiatus*, *Dichogr. octobrachiatus*, &c., have a long vertical range extending through the Dichograptid Fauna as here restricted and even beyond. What little reliable information is available concerning relative generic abundance at successive levels does not seem very encouraging for widespread correlation.

All these factors combine to discredit the former scheme of faunal subdivision and to make hazardous any alternative proposals. The Dichograptid Fauna as a whole remains a satisfactory and readily recognizable assemblage of species belonging to a wide range of multiramous and pauciramous dichograptid genera, and the fact that practically everything belongs to a single family gives it unity. It is not so well differentiated from the underlying Anisograptid Fauna but that uncertainty can exist, for example, as to the correct placing of the La 2 fauna in Australia, but that is inevitable from the close relations of the Dichograptidae to the Anisograptidae. What is in doubt is whether any general principle of universal subdivision can profitably be attempted. Short of any formal scheme, however, it may be noted that *Clonograptus* species and *T. approximatus* frequently occur in abundance near the base of the Fauna; that declined didymograptids and *Phyllograptus* are well represented near the middle; and that the first appearance of tuning-fork didymograptids (*protobifidus* and allied forms) and *Isograptus* reliably indicate the upper part (with *Glyptograptus dentatus*, *Cardiograptus*, and *Oncograptus* locally). Zoning, on a regional basis, has proved entirely reliable, and the zoning of the Bendigonian, Castlemainian, and Chewtonian of Victoria is an almost ideal example, but exact correlation over long distances may not always be easy.

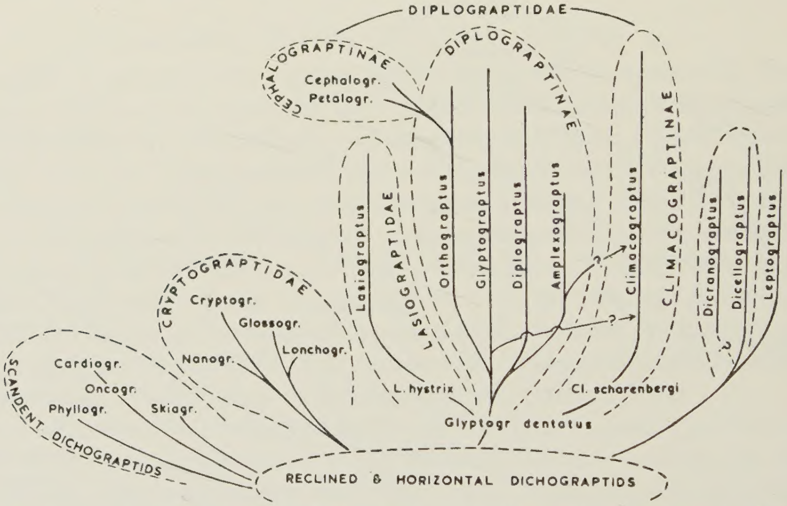


TEXT-FIG. 1. Diagram illustrating tentatively the phylogeny of *Tetragraptus* and *Didymograptus*. (Reproduced from *Treatise on Invertebrate Paleontology*, Pt. V, fig. 49.)

3. THE DIPLOGRAPTID FAUNA

Introduction. In Britain, the Diplograptidae make their first appearance with *Glyptograptus dentatus* near the top of the Arenig, being known from the Shelve Church Beds and the *hirundo* zone of Shropshire, the upper part of the *extensus* and the *hirundo* zones of the Skiddaw Slates, and the *hirundo* zone of Anglesey. The spread of this and allied forms (such as *Amplexograptus* and *Climacograptus*) is rapid (see text-fig. 2), and coincides with the rise of *Cryptograptus* and *Glossograptus* to form a distinctive biserial association in the *bifidus* fauna. Their presence in this country is to a great extent masked by the extraordinary profusion of tuning-fork graptolites; but subtract these pendent didymograptids from any representative Llanvirn Fauna and there remains a distinctive diplograptid element.

That this is equally true of Scandinavia is clearly brought out in the memoirs of Ekström (1937) and Hede (1951, p. 48) for south Sweden, and Størmer (1953, p. 44) for the Oslo area. It also applies to the Lower Llanvirn of Belgium (Bulman 1950*b*), though not so satisfactorily to France and Bohemia.



TEXT-FIG. 2. Diagram illustrating tentatively the phylogeny of the principal genera of biserial graptolites. *Amplexograptus* should have been shown as originating independently from *Glyptogr. dentatus* before *Diplograptus*. (Reproduced from *Treatise on Invertebrate Paleontology*, Pt. V, fig. 50.)

A diplograptid fauna closely similar to that of north-west Europe is again represented in the *dentatus* beds of Levis and Deepkill, where it overlies the *bifidus* beds (Raymond's zones C2 and C3, and Deepkill beds 3–5). I suggest that these *dentatus* beds are the true equivalent of our Lower Llanvirn, from which it would follow that the *bifidus* zone of eastern North America is to be correlated with our Upper Arenig. No biserial graptolite of any kind is known below the *dentatus* zone in eastern North America, where the *bifidus* zone is exclusively dichograptid; and the limited composition of the biserial element in the *dentatus* zone itself implies a position near the base of the Diplograptid Fauna. It seems to me that the correlative value attaching to the diplograptids is superior to that of *D. bifidus*, which is an intermediate member of an unusually slowly evolving stock (*protobifidus–bifidus–murchisoni*), to the successive stages and offshoots of which it is notoriously difficult to give precise definition.[1]

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[1] In the zonal and other repercussions of this view, it must not be overlooked that the type of *D. bifidus* (Hall) came from the Levis Shales of Quebec.

The recognition of what appears to be *D. bifidus* 'identical with that at Levis' in the *Oncograptus–Cardiograptus* series of Marathon by Berry (*in litt.* 1957) would on this view agree with the position allotted to the Yapeenian by Harris and Thomas (1938), and with the record of *Oncograptus* associated with an (admittedly fragmentary) Arenig fauna in western Ireland (Cummins 1954).

There is, however, one record (Simpson Group of Oklahoma, Decker 1935) in North America of the association of a pendent didymograptid (*artus*) with a biserial form ('*Amplexograptus maxwelli*'), and in a later paper Decker (1941) suggested that the Deepkill species might perhaps be *protobifidus*.

In South America (Bulman 1931; Lemon and Cranswick 1956), *Glyptograptus*, *Amplexograptus*, and cryptograptids are abundantly associated with pendent didymograptids in assemblages of Llanvirn age, but the collections reported upon lack a proper stratigraphical control.

In Australia, the pendent dichograptid series (*Tetragr. fruticosus*, *D. protobifidus*), after being so well developed and zonally important in the Bendigonian and Castlemainian, ends abruptly in the overlying beds. There are no representatives of *D. bifidus* or *murchisoni*, and the early diplograptid fauna of Harris and Thomas's 'Middle Ordovician' (M.O. 1–4) is rendered all the more conspicuous by their absence. It is of interest to note here that the form described by Ekström as *A. maxwelli* from the *bifidus* zone of Sweden is identified by Hede (1951, p. 48) and Nilsson (1951) as *A.* cf. *differtus* H. and T. from M.O. 2.

From the Kopalinski beds of the Chu-Iliiski mountains of Kazakhstan, Keller (1956) has described a fauna consisting of *Diplograptus*, *Climacograptus*, *Cryptograptus*, *Glossograptus*, and *Trigonograptus* associated with *Loganograptus*, *T. quadribrachiatus*, and a few extensiform didymograptids which he correlates with the Llanvirn. The index fossils of the two zones which he recognizes are biserial forms; and biserial graptolites are used as zonal and subzonal indices in the Ningkuo Shale for a fauna which Hsü (1934), in my opinion rightly, correlates with the *bifidus* zone.

This then is the evidence on which it is claimed that the Diplograptid Fauna, logically defined, begins at the base of our Llanvirn, the Upper Didymograptus Shales of Scandinavia, the *dentatus* zone of eastern North America, and the 'Middle Ordovician' of Australia. Its upper limit remains the same as that of Elles 1922, for it persists until in turn replaced by the development of monograptids in the *vesiculosus* zone of the Lower Llandovery. The total fauna is extremely diversified, embracing the gradual development and waning of various elements, which permit the recognition of four subfaunas, but the boundaries between them are seldom sharp.

A. *The Glypto-Amplexograptid Subfauna*

To those accustomed to having the emphasis firmly placed on pendent didymograptids the name given to this subfauna may strike a jarring note; but, with the possible exception of French and Bohemian Llanvirn, the diplograptid element is important and in many parts of the world tuning-fork graptolites have already disappeared before its commencement.

On my interpretation, the base of this (and hence of the Diplograptid Fauna) is not marked by the incoming of *Glyptograptus dentatus* (which occurs in the *extensus* zone and may locally be quite abundant in the *hirundo* zone[1]), but by its association with other diplograptid genera. Species of *Glyptograptus*, *Amplexograptus*, and *Climacograptus* are characteristic; *Diplograptus* s. str., *Hallograptus*, and *Lasiograptus* may also occur, together with *Cryptograptus* and *Glossograptus* (see text-fig. 2), and the enigmatic *Trigonograptus* may persist into the lower beds.

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[1] D. E. Jackson (1956) records nearly 50 per cent. of *G. dentatus* in the *hirundo* zone faunas of the Skiddaw Slates at some localities.

Dichograptids are represented, especially in the lower part of the subfauna, by the 'tailings' of the Dichograptid Fauna, and near the base commonly outnumber the diplograptid element. They include horizontal, declined, and pendent didymograptids, *Tetragraptus*, *Dichograptus*, *Loganograptus*, *Phyllograptus*. and the multiramous *Pterograptus*, *Trichograptus*, and *Brachiograptus*. In any one region, they are not as a rule so well represented as this collective list would suggest. For example, in Britain, declined and especially pendent *Didymograptus* form the bulk of the dichograptid element; in Scandinavia, pendent forms in profusion are characteristically associated with *Pterograptus* and *Janograptus*; in Australia, the pendent didymograptids are conspicuously absent, but declined forms with some *Tetragraptus*, *Pterograptus*, and *Brachiograptus* appear to make up the bulk of the non-diplograptid assemblage; in the *dentatus* zone of North America, the dichograptid element consists of extensiform didymograptids, *Tetragraptus*, *Dichograptus*, and rather commonly *Loganograptus*.

Dicellograptus makes its first appearance in this subfauna, being reported from as low as the *bifidus* zone in Britain (*D. moffatensis*) and rather higher in Sweden (*D. vagus*). *Dicranograptus* appears in the uppermost part (*D. rectus* in Britain and *D. irregularis* in Sweden).

Focusing attention on the Diplograptid element results in linking faunally the Llanvirn with the Llandeilo, for the palaeontological break between the *murchisoni* and *teretiusculus* zones (Elles 1940, p. 411) is little more than the extinction of tuning-fork graptolites. In consequence, diplograptids come to dominate the upper part of the fauna almost completely, but the Llandeilo diplograptid element contains nothing new above specific level. It also gives some support to Størmer's choice (1953) of this horizon as marking the base of the Middle Ordovician, corresponding with Australian practice.

B. *The Nema-Dicellograptid Subfauna*

Here we find a fairly sharp and certainly easily recognizable base with the incoming of *Nemagraptus gracilis*, and with this also the whole character of the fauna changes; *Dicellograptus* and *Dicranograptus* species now assume numerical importance and even dominance. In the *gracilis* zone of Britain, there are listed (Lapworth, Elles, andWood) eight species of *Dicellograptus* and five of *Dicranograptus*; in the *peltifer* zone, nine of *Dicellograptus* and ten of *Dicranograptus*. Coinciding with this also is the first appearance of *Leptograptus*. Diplograptids are still more abundant (nineteen species are listed in Lapworth, Elles, and Wood for the *peltifer* zone), but the only significant generic change in this element of the fauna is the appearance of rare *Orthograptus*.

Scandinavia, North America, Australia, and China all furnish closely analogous assemblages. *N. gracilis* itself has an almost worldwide distribution; *Dicellogr. sextans*, *C. peltifer*, and many others are also remarkably widespread and together give the impression of unusually free inter-communication at this time.

C. *The Ortho-Dicellograptid Subfauna*

I use this term to include the remainder of the Ordovician portion of the Diplograptid Fauna, which comprises various species of *Orthograptus* associated principally with

Dicellograptus, *Dicranograptus*, *Leptograptus*, and *Climacograptus*. Its lower limit coincides with the appearance of *Orthograptus* in abundance represented by the *truncatus*, *calcaratus*, and *quadrimucronatus* groups; its upper limit with the final disappearance of axonolipous graptolites.[1] *Orthograptus*, *Climacograptus*, and *Dicellograptus* range throughout, but *Dicranograptus* and *Leptograptus* are restricted to the lower portion.

The above association renders an assemblage of this age readily identifiable,[2] but there may be some uncertainty as to the base of the subfauna. Thus the *vasae* and *molestus* zone faunas of Sweden and the *wilsoni* zone fauna of Scotland would be assigned to the underlying subfauna on general faunal characteristics, while the assemblages from the upper part of the *multidens* shales of Shropshire and south Wales might be identified as belonging to this subfauna on account of their rather more conspicuous orthograptid element. But faunal assemblages at this horizon have proved difficult to the specialist employing the full resources of zonal correlation (Jaanusson and Strachan 1954), and Nilsson (1953) has recorded a peculiar mixed assemblage from Sularp (Scania) which suggests a transitional fauna between the *gracilis* and *clingani* zones.

Pleurograptus linearis has a curious distribution, occurring abundantly in south Scotland, but not elsewhere in Britain or in Europe, yet it is recorded from North America and Australia. The more widely distributed *C. styloideus* has been used as an alternative index fossil, and most of the species characteristic of the lower part of the subfauna are widely distributed.

The upper part of this subfauna has everywhere the characters of an impoverished fauna, with dwarf varieties of *Climacograptus* and *Orthograptus* associated with the last survivors of *Dicellograptus*. The index fossil of one zone (*complanatus*) is, however, a remarkably widespread species, recorded from many areas in North America, Europe, Asia, and Australia.

D. *The Ortho-Climacograptid Subfauna*

This small subfauna is closely linked, even to a considerable degree of specific identity, with the subfaunas above and below, and is in all respects transitional though it can very easily be defined. Like all Silurian graptolite assemblages, it is composed solely of scandent forms, but the genus *Monograptus* has not yet appeared, so that it is entirely biserial or uni-biserial. I have named it the Ortho-Climacograptid Subfauna, but one of its most characteristic features is the reappearance of *Glyptograptus* and *Diplograptus* (= '*Mesograptus*'). Whether these are generically identical with their Ordovician namesakes is perhaps questionable; the gap between Ordovician and Silurian *Diplograptus* has been almost bridged by some rare forms described by Davies (1929) from the *linearis* and *complanatus* zones, but there is no sign of *Glyptograptus* between the *wilsoni* and *anceps* zones.

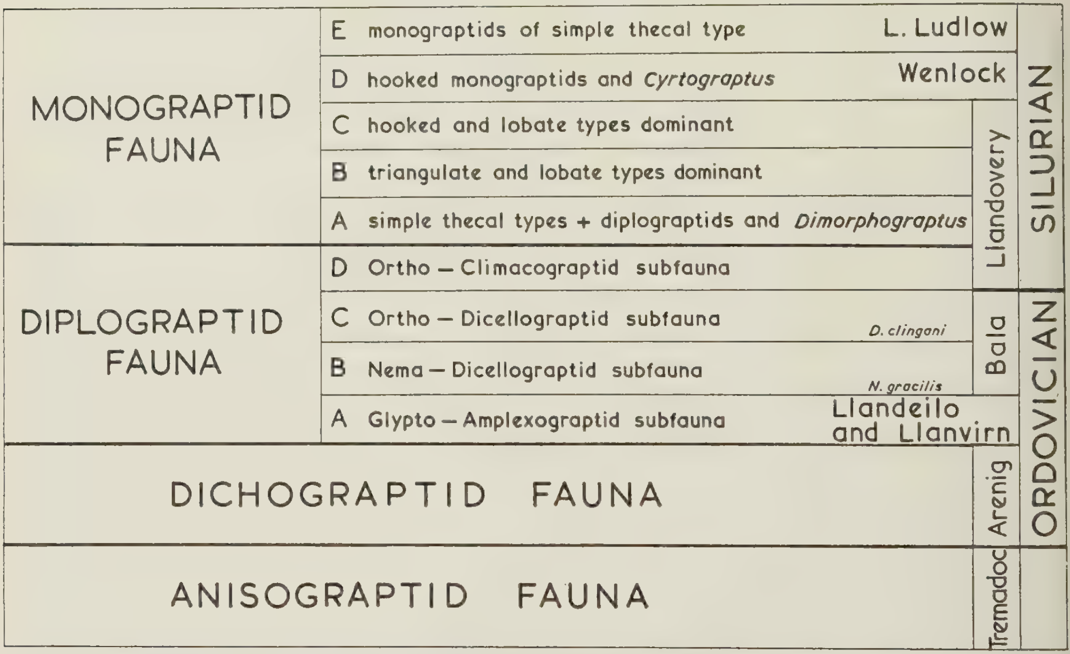
Structural modifications at the proximal end beginning at this horizon lead to the production of such genera as *Akidograptus* and *Dimorphograptus*; the first of these is confined to the base of this subfauna and is widely distributed, the latter only becomes abundant in beds above, where it is also joined by *Rhaphidograptus*.

[1] Axonolipa was a term proposed by Frech (and adopted by Ruedemann) for graptolites without a virgula (i.e. graptolites with an exposed nema), in contradistinction to the Axonophora or graptolites with a virgula. It thus furnishes a convenient comprehensive term for all other than scandent graptolites.

[2] In American faunal lists (e.g. Ruedemann 1947), the abundance of *Orthograptus* is very often concealed by the mistaken reference of such species as *quadrimucronatus* to *Glossograptus*, and various members of the *truncatus* group to *Amplexograptus*.

4. THE MONOGRAPTID FAUNA

No changes are here proposed in the definition or subdivision of this fauna as outlined by Miss Elles (p. 159). The thecal elaboration trends used at this level have proved more reliable than the others. This may be partly the result of a less exacting time-scale, and the total assemblage is less complicated, for whether or not *Monograptus* be polyphyletic, it certainly does not compare with the intricate plexus of dichograptid descent.


MONOGRAPTID FAUNA
E monograptids of simple thecal type
L. Ludlow
D hooked monograptids and *Cyrtograptus*
Wenlock
C hooked and lobate types dominant
B triangulate and lobate types dominant
A simple thecal types + diplograptids and *Dimorphograptus*
Llandovery
SILURIAN
DIPLOGRAPTID FAUNA
D Ortho — Climacograptid subfauna
C Ortho — Dicellograptid subfauna
D. clingani
B Nema — Dicellograptid subfauna
N. gracilis
Bala
A Glypto — Amplexograptid subfauna
Llandeilo and Llanvirn
DICHOGRAPTID FAUNA
Arenig
ORDOVICIAN
ANISOGRAPTID FAUNA
Tremadoc

TEXT-FIG. 3. Simplified diagram showing the succession of graptolite faunas and subfaunas, related to the standard British Lower Palaeozoic succession.

The Llandovery succession of simple thecal type (associated with diplograptids), followed in turn by dominantly triangulate and isolate, and dominantly hooked and lobate, has never been seriously questioned. These subfaunas are widely distributed, but it is of interest to note how poorly developed are the faunas of this age in North America, where *Dimorphograptus*, *Cephalograptus*, *Petalograptus*, *Rastrites*, and such common species as *M. triangulatus* and *M. lobiferus* are as yet unknown (Ruedemann 1947). There is evidence, however (Thorsteinsson *in litt.*), that they are well represented in arctic Canada.

The cyrtograptid element associated with hooked monograptids characteristic everywhere of the graptolitic Wenlock, has a more restricted distribution, but the final graptolitic subfauna of the Lower Ludlow is again widespread. The complicated cladia-bearing genera *Linograptus* and *Abiesgraptus* occur in the Ludlow, and *Monograptus* trails away with such species as *uniformis* and *hercynicus* in the Upper Ludlow of Thuringia and Bohemia.

The faunas proposed are shown in outline in text-fig. 3, and are defined in rather more detail below.

4. MONOGRAPTID FAUNA

Scandent uniserial rhabdosomes (Monograptidae) with diplograptids in lower part and subordinate retiolitids throughout.

- E. L. Ludlow: monograptids of simple thecal type.
- D. Wenlock: cyrtograptids and hooked monograptids.
- Llandovery
  - C. Monograptids with hooked and lobate thecae: *sedgwicki* to *crenulatus* zones.
  - B. Monograptids with triangulate and isolate thecae: *gregarius* and *convolutus* zones.
  - A. Monograptids of simple thecal type: diplograptids and dimorphograptids abundant in lower part: *vesiculosus* (*atavus* and *acinaces*) and *cyphus* zones.

3. DIPLOGRAPTID FAUNA

Comprises main development of Diplograptidae, Lasiograptidae and Archiretiolitinae with cryptograptids: development and extinction of *Dicellogr.* and *Dicranogr.*, and at base last dichograptids.

- D. Ortho-Climacograptid subfauna: diplograptids (including *Glyptograptus* and *Diplograptus*) with *Akidogr.* and *Dimorphogr.*: *persculptus* and *acuminatus* zones.
- C. Ortho-Dicellograptid subfauna: diplograptids (especially *Orthograptus*, *Climacograptus*) with *Dicellogr.*, *Dicranogr.*, and *Leptogr.* in lower part, and *Dicellogr.* in upper part: *clingani* to *anceps* zones.
- B. Nema-Dicellograptid subfauna: abundant diplograptids (incl. *Diplograptus*) with *Dicellogr.*, *Dicranogr.*, and *Leptogr. N. gracilis* in lower part: *gracilis* to *wilsoni* zones.
- A. Glypto-Amplexograptid subfauna: early species of most diplograptid genera, especially *Glyptogr.* and *Amplexogr.*, with *Cryptogr.*, *Glossogr.* and late dichograptids: *bifidus* to *teretiusculus* zones.

2. DICHOGRAPTID FAUNA. An exclusively dichograptid assemblage of multiramous and pauciramous genera, except for *Clonograptus* and *Bryograptus* near base and *G. dentatus* in highest portion: *extensus* (*deflexus*, *nitidus*, *gibberulus*) and *hirundo* zones.

1. ANISOGRAPTID FAUNA. A dendroid assemblage characterized by siculate *Dictyonema* associated with and followed by pendent and horizontal anisograptids (*Anisogr.*, *Staurogr.*, *Clonogr.*, *Bryogr.*, *Triogr.*, &c.); some small didymograptids are known: L. Tremadoc (*Dictyonema* Shales) and U. Tremadoc (3$a\beta$ Norway; ? La 2 Austr., &c.)

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PERMIAN CORALS FROM NORTHERN IRAQ

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ABSTRACT. Rugose corals from the Zinnar Limestone Formation (Artinskian) of northern Iraq are allocated to the Waagenophyllidae fam. nov. and grouped as Waagenophyllinae Wang 1950 (redefined) or Wentzelellinae subfam. nov. The lower part of the formation, with abundant *Polydiexodina*, is of *Parafusulina* age and the upper of possible *Neoschwagerina* age. New morphological terms for the rugose corals are explained and *Ipciphyllum ipci* gen et sp. nov. and *Wentzellophyllum* gen. nov. are described. *Michelinia favositoides* Girty is re-established as a valid species.

INTRODUCTION

THE Permian strata of Kurdistan, northern Iraq, are of Tethyan facies and faunal phase, closely comparable to the Permian strata of the neighbouring areas of Anatolia and Iran, and with faunal links with the more distant successions of the Productus Limestones of northern Pakistan and the Maokou and Chihsia Limestones of southern China. They are completely exposed, and reasonably accessible, from their unconformable junction with Lower Tournasian limestones and shales to a possible passage junction with the Trias. They are almost entirely limestones, variously fossiliferous. Their upper part contains a sporadic *Bellerophon* fauna and their lower part a Productid-bryozoan fauna with corals. Fusulines occur in the lower part and calcareous algae occur sporadically throughout.

In the latter parts of 1948 and 1951, R. Wetzel and D. M. Morton, geologists of the Iraq Petroleum Company, during reconnaissance surveys of northernmost Iraq, measured two sections of these Permian limestones and made a small collection of fossils. The author made two visits to the area and took part in these surveys. This account of the corals is one of a series describing the fauna then collected. The loan to the author by J. M. Edmonds, Curator of the Geological Collections of the University Museum, Oxford, of the thin sections of the Permian corals of Iran described by Douglas in 1936 and 1950 has greatly assisted the naming of the Iraq corals. The work has been carried out in the Geological Laboratories of the Iraq Petroleum Company and its publication has been generously authorized by its Directors and Chief Geologist. To all the above the author here records his thanks. All the specimens described in this paper have been presented to the British Museum (Natural History): their individual registrations are here recorded by numbers preceded by the letter R.

LOCATION AND FAUNAL STRATIGRAPHY

About 100 km. north of Mosul and between the Tigris and the Greater Zab rivers, the Iraq–Turkish boundary forms a northern embayment (approx. north of 37° 15′) which brings into Iraq the continuation of a southern foreland range of the Taurus Mountains consisting of an upthrust east–west asymmetrical anticline of Permian limestones flanked north and south by Triassic limestones, dolomites, and shales. In the west the range is crossed by the Khabour River, a tributary of the Tigris, and in the east by the Geli Khana, a tributary of the Greater Zab. Between them the range rises to the peaks of Chia-i-Zinnar (7,390 ft.) in the west and the Zozan-i-Harrur (7,900 ft.) in the east. To

[Palaeontology, Vol. 1, Part 3, 1958, pp. 174–92 , pls. 32–35.]

the east of the Geli Khana there is the peak of Jebel Satina (8,465 ft.). The gorges cut by the Khabour and Geli Khana rivers expose two inliers of pre-Permian rocks, the western inlier with the villages of Chalki (Chalki Islam and Chalki Nasura) and the eastern with the village of Ora, the two villages being about 20 km. apart. The Permian limestones were measured mainly in two sections, the one north from Ora along the Geli Khana gorge and across the northern flank of the anticline, the other north of Harrur (16 km. west of Ora) over the saddle between Chia-i-Zinnar and Zozan-i-Harrur to Darari summer village. It was from these two sections that most of the fossils described in this paper were collected.

The Permian succession is 760 m. thick in the Harrur section where there is possibly a strike fault and 811 m. in the Geli Khana section. It is divided into three formations: an upper one, the Darari Formation, 296 m. thick at Harrur and 318 m. at Geli Khana; a middle one, the Satina Formation (name chosen by Wetzel and Morton), 77 m. at Harrur and 61 m. at Geli Khana; and a lower one, the Zinnar Formation, 387 m. at Harrur and 432 m. at Geli Khana. They are all limestone formations except that the lowest 12·4 m. of the Zinnar Formation is a limestone–mudstone series. The junction of the Zinnar Formation with the underlying Tournaisian (Z–C_1) limestone is a haematitic and pitted but fairly level surface. The Tournaisian limestone is dated by an abundant brachiopod-bryozoan-coral fauna including *Caninia cornucopiae* vars. Mich., *Zaphrentites parallelus* (Carr.), *Z. delanouei* (Ed. and H.), *Fasciculophyllum* cf. *omaliusi* (Ed. and H.), *Michelinia gracilis* Smyth, *M.* aff. *megastoma* Phillips, *Vaughania cleistoporoides* Garw., *Actinoconchus lamellosus* (Léveillé), *Camarotoechia* cf. *letiensis* (Gosselet), *Chonetes* (*Plicochonetes*) *crassistria* (M'Coy), *Dictyoclostus vaughani* (Muir-Wood), *? Plectospirifer strunianus* (Gosselet), *Rhipidomella michelini* (Léveillé), *Spirifer* aff. *tornacensis* de Kon., *Syringothyris cyrtorhyncha* North, *Tylothyris* cf. *laminosa* (M'Coy), *Phillipsia strabonsis* Frech.

The Darari Formation has an occasional *Bellerophon*-Productid-bryozoan fauna but like the Satina Formation is generally unfossiliferous. An exception is a bed of limestone 77 m. from the top of the Permian which contains abundant *Amblysiphonella* and *Steinmannia*. It also has towards its upper part various faunas of thin-shelled lamellibranchs which suggest that its faunal phase is approaching that of the overlying Trias into which it may possibly directly pass. The lower part of the Trias contains a fauna which dates it as of Werfenian age. It includes *Anodontophora fassaensis* Wissman, *Myophoria balatonsis* Frech, *Pseudomonotis* (*Claraia*) *aurita* (Hauer), *P.* (*C.*) *clarai* Emmrich, and *Spirorbis valvata* Goldfuss from lower beds; and *Anodontophora fassaensis* Wissman, *A. fassensis* var. *bittneri* Frech, *Gervillia sp.*, *Myophoria balatonsis* Frech, *M. ? laevigata* Zieten, *M. praeorbicularis* Bittner, and *Pseudomonotis* (*Claraia*) *aurita* Hauer from beds above.

The following calcareous algae have also been recorded from the Zinnar Formation (Elliott, 1955, 1956): *Diplopora sp.*, *Gymnocodium bellerophontis* (Rothpletz), *Macroporella sp.*, *Mizzia velebitana* Schubert, *Permocalculus digitatus* Elliott, *P. forcepinus* (Johnson), *P. fragilis* (Pia), *P. plumosus* Elliott, *P. tenellus* (Pia), and *P. solidus* (Pia). *Mizzia* is very common in the Polydiexodina limestones.

The corals are most abundant about the middle of the Zinnar Formation where limestones, known as the Wentzelella Limestones, contain productids and other brachiopods, bryozoans, and large massive corals all entirely or partly silicified. In the Geli

Khana section, they are 16·5 m. thick and 202 m. below the Satina Formation: in the Harrur section, they are 14·9 m. thick and 236·9 m. below the Satina. Corals also occur in the lowest part, 65 m. or so, of the Zinnar Limestone though they have only been collected from the top 17 mm., the Michelinia beds. In the Geli Khana section these beds are 203·8 m. below the Wentzelella Limestones. They are not exposed in the Harrur section but are well exposed on the slopes of Chia-i-Zinnar above Kaista. In the 203·8 m. between the Wentzelella and Michelinia Limestones corals are rare except in the Geli Khana section where 26·70 m. above the Michelinia beds there is a limestone with corals from which the '*Lonsdaleia*' and *Waagenophyllum*, described later, probably came. The lower part of the Zinnar Limestone, about 65 mm. and including the Michelinia Limestones contains abundant fusulines. These are mainly *Polydiexodina persica* Kahler (Kühn 1933), a species which has already been recorded as abundant in the lower part of the Permian of Persia (Douglas 1936, 1950) and which also occurs in Afghanistan (Dunbar 1933). Other fusulines have also been found in these beds, notably *Parafusulina kattaensis*, the characteristic form of the Lower Productus Limestone (Dunbar 1933) and also found in the Polydiexodina beds of Persia (Douglas 1950). These beds have been allocated to the Parafusulina Zone as should be the lower part of the Zinnar Limestone.

AGE AND CORRELATION

The corals collected from the Wentzelella Limestones include *Wentzelella canalifera* (Mansuy), *W. socialis* (Mansuy), *Wentzellophyllum persicum* (Douglas), *Polythecalis sp.* cf. *P. japonica* Yabe and Minato, *Ipciphyllum ipci* sp. nov., *I. elegans* (Huang), *I.* cf. *subtimoricum* (Huang), *I.* cf. *timoricum* (Gerth). Ten specimens of *Ipciphyllum ipci* were collected, the remainder are represented by one or two specimens. Only *Michelinia favositoides* Girty and *M.* cf. *siyangensis* Reed were collected from the Michelinia beds though other corals do occur there. Two specimens, both from the scree of the considerable thickness of limestone between the above two horizons, are named *Waagenophyllum indicum* (Waagen and Wentzel) var. nov. and '*Lonsdaleia*' *chaoi* (Huang) var.; they probably come from the lower part of this limestone series.

The fusulines and the other fossils have not yet been seriously examined and therefore no foraminiferal age-evidence is available other than the allocation of the Michelinia Limestones to the Parafusulina Zone. Stratigraphical position suggests that the limestones with *Waagenophyllum* and '*Lonsdaleia*' could also be included in this Zone.

The *Waagenophyllum-Wentzelella* faunas are generally considered to be limited to the Sakmarian-Artinskian-Kungurian (Hill 1948, 1957) though their relative positions within that succession are not established with any certainty. Huang (1932) in his description of the corals of the Chihsia and Maokou Limestones of southern China grouped them into five faunas designating them by the following index fossils and listing characteristic fossils.

Maokou Lmst.	*Lophophyllidium kayseri* (Huang)
	Ipciphyllum timoricum (Gerth)
Chihsia Lmst.	*Polythecalis yangtzeensis* Huang
	Hayasakaia elegantula (Y. and H.)
	Wentzellophyllum volzi (Y. and H.)

The '*volzi*' fauna seems to have distinct entity and to be widely distributed in the

Tethyan Permian. The index species occurs in the Carnic Alps (Felser 1937), Anatolia (Bali Maaden, Enderle 1900), southern China (Huang 1932), Japan (Minato 1955) as *Stylidophyllum yokoyamai* (Ozawa). Its associate, *S. kueichowense* Huang, which differs very little from it, occurs in Persia (Douglas 1936, 1950) with *Waagenophyllum* aff. *indicum* (W. and W.), *Polydiexodina*, and *Parafusulina*. It also occurs in the Permian of Ala Dagh, north of Tarsus, Anatolia (Heritsch 1939). '*Lonsdaleia*' *chaoi* occurs in this fauna in the Chihsia Limestone. It seems most probable that the '*Lonsdaleia*' *chaoi* and *Waagenophyllum* cf. *indicum* of northern Iraq are part of the '*volzi*' fauna. The fauna has not been recorded from the Productus Limestones of Pakistan.

The *Hayasakaia* (*Tetrapora* auctt.) and *Polythecalis* faunas are usually grouped together. In this fauna *Wentzelella* and various species of *Ipciphyllum* are abundant. They include *W. canalifera* (Mansuy) from Cambodia, also recorded from the Middle Productus Limestone of the Salt Range, and *Ipciphyllum subtimoricum* (Huang) and allied forms from Timor, Japan, southern China, Salt Range, Afghanistan, Persia, Anatolia, Serbia, Carnic Alps, and Sosio. The fauna is generally that of the Wentzelella Limestones of Iraq. In many of the above localities *Neoschwagerina*, especially *N. cratulifera* (Schwager) occurs associated with this coral fauna, which could quite well be the age of the Wentzelella Limestones of Iraq.

The '*timoricum*' fauna has rarely been identified with certainty west of China and Japan where it is placed in the Yabeina Zone.

MORPHOLOGICAL AND SYSTEMATIC PALAEONTOLOGY

Structural terms

Dissepitheca (scelerotheca *auctt.*). Vertical wall dividing the tabularium from the dissepimentarium. Formed by the thickening of the innermost surface of the dissepiments. Usually forms the bounding wall of the calicular pit. (Pl. 34, figs. 5, 6.)

Crestal septa (Lonsdaleoid septa *auctt.*). Septal ridges, radially continuous, on dissepimental surfaces (usually inclined inwards) replacing normal septa by vertically discontinuous plates. May be extensions of septa of central part of corallite or of septal ridges (denticles) of epitheca. (Pl. 35, figs. 1, 7.)

Crestal septal lamellae. Vertical ridges on surfaces of axial tabellae (usually inclined outwards) replacing normal septal lamellae by vertically discontinuous plates. (Pl. 35, fig. 5.)

Dissepiseptum. Linear arrangement of small lateral dissepiments replacing septum in dissepimentarium. (Douglas 1950, text-figs. 1*a*, *c*.)

Transverse tabulae. Tabulae horizontal or approximately so in tabularium. May be simple or compound, flat, with or without upturned edges, or shallowly curved, proximally or distally, or cystose. (Pl. 35, figs. 2, 3.)

Clinotabulae. Tabulae, vertical or steeply inclined downwards to axis, usually interseptal. May be simple, flat, or shallowly curved (convex surface towards axis) and continuous with transverse tabulae, or compound or elongate-cystose. May simulate dissepiments. (Pl. 33, fig. 4; Pl. 35, fig. 2.)

Clinotabularium. Tabularium with clinotabulae. Usually forms an outer zone of tabularium adjacent to dissepitheca and often sharply distinguished from an inner (periaxial) zone of transverse tabulae. (Pl. 33, fig. 4; Pl. 34, fig. 5.)

WAAGENOPHYLLIDAE fam. nov.

Rugosa, solitary or compound (phaceloid to aphroid). Septa of two or more orders, may be crestal, naotic or dissepisepta. Axial column lonsdaleoid. Tabularium of periaxial transverse tabulae and outer zone of clinotabulae. Dissepimentarium may be interseptal, crestal-septate, or non-septate.

Remarks. The rugose corals of the Permian which were originally placed in the genus *Lonsdaleia* and later transferred to such genera as *Waagenophyllum* and *Wentzelella* are still usually retained in the Lonsdaleiidae though Wang (1950) has recognized their individuality by placing them in a subfamily, the Waagenophyllinae. Recent work, however, has shown that many Permian forms have developed new structures, many have more than two orders of septa and all of them are characterized by an inner and outer tabularium, distinctions which justify their family separation from the Lonsdaleiidae. Within the new family there is one group with simpler structure and only two orders of septa, and another with more complex structure and three or more orders of septa. Both groups have apparently developed independently along the trend from phaceloid to aphroid corallites and they are therefore in each recognized as a subfamily.

WAAGENOPHYLLINAE Wang 1950

Diagnosis. Waagenophyllidae with simple septa of two orders. Clinotabularium, usually distinct, of very steeply inclined clinotabulae, usually cystose.

WAAGENOPHYLLUM Hayasaka 1924

Type species *Lonsdaleia indica* Waagen and Wentzel 1886

Waagenophyllinae of slender phaceloid corallites. Tabularium, occupying greater part of corallite, formed of wide outer zone of elongate, almost vertical, cystose clinotabulae and very narrow periaxial zone of transverse tabulae. Narrow interseptal dissepimentarium of small, almost vertical, strongly curved, dissepiments.

Waagenophyllum indicum (Waagen and Wentzel) var. nov.

Plate 33, figs. 4, 9

COMPARE

Lonsdaleia indica Waagen and Wentzel 1886, p. 897, pl. 101, figs. 1–3, p. 115, figs. 3, 4; Diener 1897, p. 82, pl. 13, figs. 5, 6; Diener 1911, p. 43, pl. 6, fig. 4 (*non* Mansuy 1912, p. 9, pl. 1, fig. 3.)
Lithostrotion jourdyi Mansuy 1912*b*, p. 69, pl. 13, fig. 5.
Lithostrotion mixtum Mansuy 1912*a*, p. 38, pl. 8, fig. 5.
Waagenella indica, Yabe and Hayasaka 1915, p. 96.

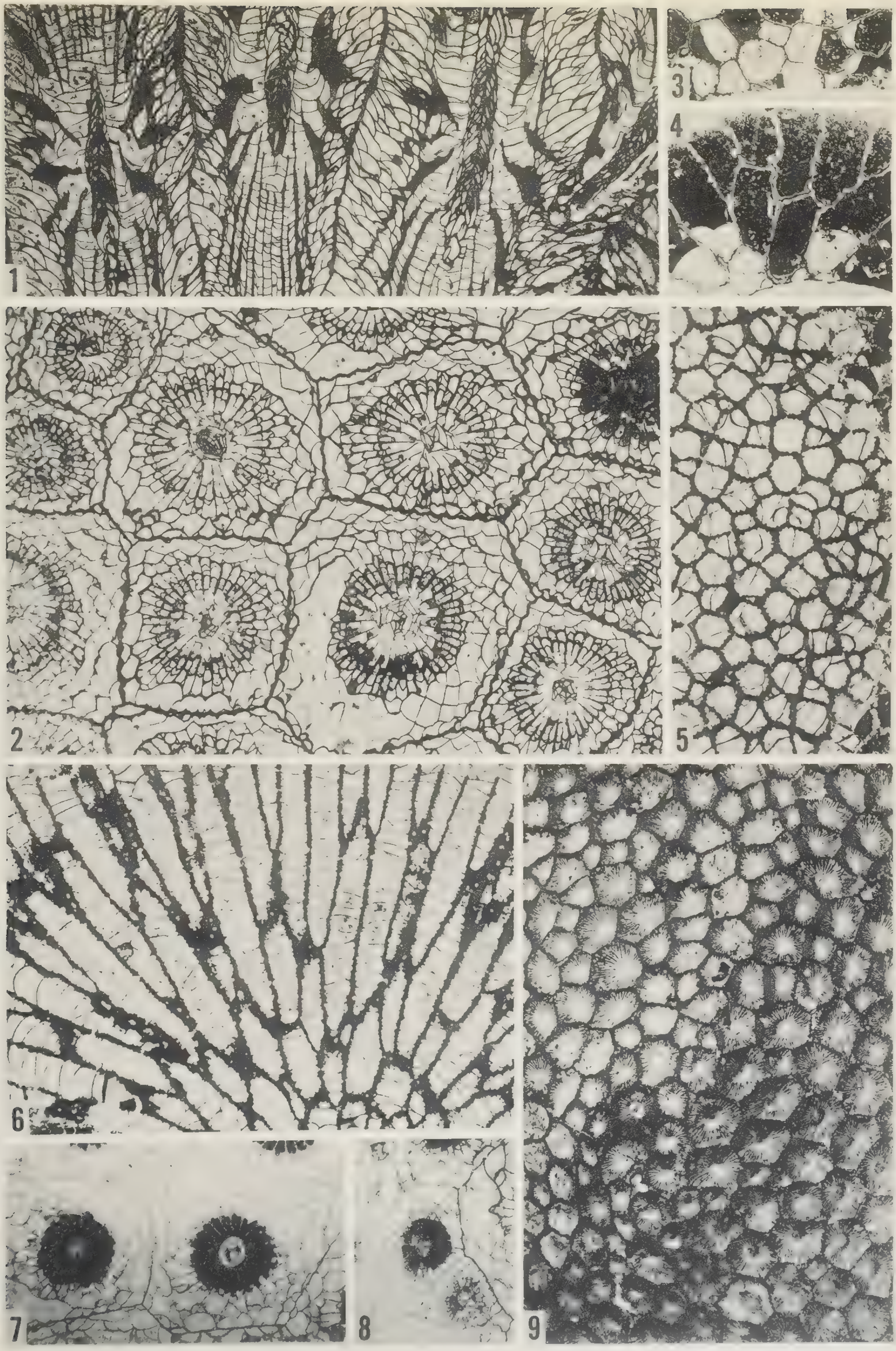
EXPLANATION OF PLATE 32

Specimens R 41997–8 are from Michelinia Limestones in the lower part of the Zinnar Limestone (Permian) of the Geli Khana section, Ora, northern Iraq. R 41996 is from about 27 m. above the Michelinia Limestones.

Figs. 1, 2, 7–9. '*Lonsdaleia*' *chaoi* Huang var. 1, vert. sect. (slightly oblique), R 41996*b*, ×3. Note, on right, new corallite starting within dissepimentarium. 4, Trans. sect., R 41996*c*, ×3. 7, 8, Both from trans. sect. R 41996*a*, ×2·4, through calices and isolated axial columns. 9, Calicular surface of corallum, R 41996, ×0·6. Walls appear thick owing to wearing away of thin edge.

Figs. 3, 4. *Michelinia sp.* cf. *M. siyangensis* Reed. 3, Trans. sect., R 41998*b*, ×2·8, note fine septal spines. 4, Vert. sect., R 41998*a*, ×3, note medial strand within walls and large pores through walls.

Figs. 5, 6. *Michelinia favositoides* Girty. 5, Trans. sect., R 41997*a*, ×3, note large pores through walls. 6, Vert. sect., R 41997*b*, ×3, note spines (as vertical lines of small dots where wall has been only just removed).



HUDSON, Permian corals

Waagenophyllum indicum, Hayasaka 1924, p. 23; Smith 1935, p. 34, pl. 8, figs. 1–6; Heritsch 1937, pl. 2, fig. 5; Soshkina *et al.* 1941, text-figs. 42–44.
Waagenophyllum virgalense var. *mongoliense* Grabau 1931, p. 42, pl. 1, figs. 8, 9.
Waagenophyllum indicum var. *kueichowense* Huang 1932, p. 48, pl. 3, figs. 1, 2.
Waagenophyllum (*Liangshanophyllum*) *wengchenense* Huang 1932, p. 50, pl. 3, fig. 3.
Waagenophyllum aff. *indicum*, Douglas 1950, p. 9, pl. 1, figs. 1, 1*a*.
Waagenophyllum indicum var. *usugenuensis* Minato 1955, p. 103, pl. 19, fig. 3, pl. 31, fig. 1.

Material. R 42007 (three pieces) and sections *a* (Pl. 33, figs. 4*a*, 4*b*) and *b* (Pl. 33, fig. 9). Scree, below the Wentzelella Limestones, Geli Khana section, Ora, northern Iraq.

Description (Iraq material). Loosely phaceloid, corallites about 6 mm. across. Generally twenty-two major septa, slightly flexuous, slightly distally thickened but not forming stereozone; reaching to, or close to, axial column to which counter septum is joined. Minor septa up to half length of major. No tertiary septa. Tabularium, about 0·75 of corallite width, consists of outer zone of vertically elongate interseptal clinotabulae and a very narrow periaxial zone of transverse tabulae. Clinotabulae concentric in transverse section, transverse tabulae encircle axial column. Dissepimentarium of two to three rows of almost vertical small rounded dissepiments, transversely concentric. No extra-septal dissepiments. Axial column cuspidate, and irregular, about 1·3 mm. across; irregular medial plate may be absent, and a few irregular septal lamellae and steep, almost vertical, overlapping axial tabellae. Lateral budding with parallel offsets; no horizontal offsets.

Remarks. Most of the forms listed above show slight differences in the width of the axial column, in the number of septal lamellae and axial tabellae, and the length of the minor septa and could justifiably be grouped as one species or as non-significant varieties. The figured type of *L. indica* (type specimen Waagen and Wentzel 1886, pl. 101, fig. 1, 1*a–d*) has a slightly wider and more complex axial column than most; the Iraq form has a narrower and simpler axial column than most and possibly could be considered a definite variant; it is not named since it is a scree specimen.

IPCIPHYLLUM gen. nov.

Type species. *Ipciphyllum ipci* sp. nov.

Diagnosis. Waagenophyllinae with cerioid coralla. Dissepiments mainly interseptal, occasionally slightly non-septate. Clinotabulae may be simple or compound and not cystose.

Remarks. Ipciphyllum is essentially a cerioid *Waagenophyllum*. The species now included in it belong to the '*timoricum*' group and were previously included in *Wentzelella*: they are structurally simpler than species of that genus lacking tertiary septa, dissepisepta, and lateral dissepiments. *Ipciphyllum ipsi* is made the type species since *I. timoricum* (Gerth) is imperfectly known.

Ipciphyllum ipci sp. nov.

Plate 33, figs. 1, 2, 3, 7, 10; Plate 35, fig. 4.

Lonsdaleia indica Mansuy 1908, p. 55, pl. 14, figs. 2, 2*a*; 1912*a*, p. 9, pl. 1, figs. 3*a–e*, pl. 2, fig. 1 (*non Lonsdaleia indica* Waagen and Wentzel 1886, p. 897, pl. 101, figs. 1–3, pl. 115, figs. 3–4; *non Wentzelella indica* Mansuy, Soshkina *et al* 1941, p. 184, pl. 42, figs. 1*a–c*).

Lonsdaleia (*Waagenophyllum*) *timorica* Ozawa 1925, p. 74, pl. 13, figs. 7–9 (*non Lonsdaleia timorica* Gerth 1921, p. 74, pl. 145, figs. 1, 2).

Wentzelella subtimorica Douglas 1936, p. 23, pl. 2, fig. 2, pl. 3, fig. 5; Heritsch 1939, p. 173, pl. 1, figs. 2, 3, pl. 2, figs. 7, 8, 15–17 (*non* Huang 1932, p. 59, pl. 4, fig. 1*a*, *b*; *non* Douglas 1950, p. 14, pl. 2, fig. 4; *non* Minato 1944, p. 105, text-figs. 1, 3; Minato 1955, p. 113, pl. 22, fig. 8 *et al.*).

Holotype. R 42028 (two pieces) and section *a* (Pl. 33, fig. 10). *Paratypes.* R 42002 (two pieces) and section *a*; R 42016 (two pieces) and sections *a*, *b*; R 42017; R 42019 (one piece) and sections *a*, *b* (Pl. 33, fig. 1); R 42021 and sections *a*, *b*; R 42022 (two pieces) and section *a* (Pl. 33, fig. 3); R 42023 and section *a* (Pl. 33, fig. 2); R 42024 (three pieces) and sections *a*, *b* (Pl. 35, fig. 4); R 42026 (five pieces) and sections *a* (Pl. 33, fig. 7) and *b*. All specimens are from Wentzelella Limestones. R 42002 from the Geli Khana section, Ora, northern Iraq. The remainder are from the Harrur section, Chalki, northern Iraq.

Description. Cerioid, with crimped epitheca, corallites polygonal, usually five- or six-sided, and up to 10 mm. across. About thirty-two to forty straight septa which may be thickened in tabularium. Minor septa usually two-thirds length of major but may be as long. No tertiary septa. Axial column arachnoid, circular, up to 1·6 mm. across, with thin medial plate, radial lamellae, and prominent tabellae. Slight dissepitheca. Tabularium narrow, inner zone of simple transverse tabulae and outer zone of overlapping cystose clinotabulae, zones of about equal width. Dissepiments curved concentric or angulo-concentric. Non-septal dissepiments may occur in corallite angles. Budding peripheral.

Remarks. The above species has been previously recorded as *Wentzelella subtimorica* Huang. It differs from that species, which is now allocated to *Ipciphyllum*, in that it has non-septal dissepiments, a wider axial column with more septal lamellae and its dissepiments are more angulo-concentric. *Ipciphyllum flexuosum* (Huang) has an axial column which is more complex and has more tabellae than *I. ipci* which also has a wider tabularium with tabulae better developed.

EXPLANATION OF PLATE 33

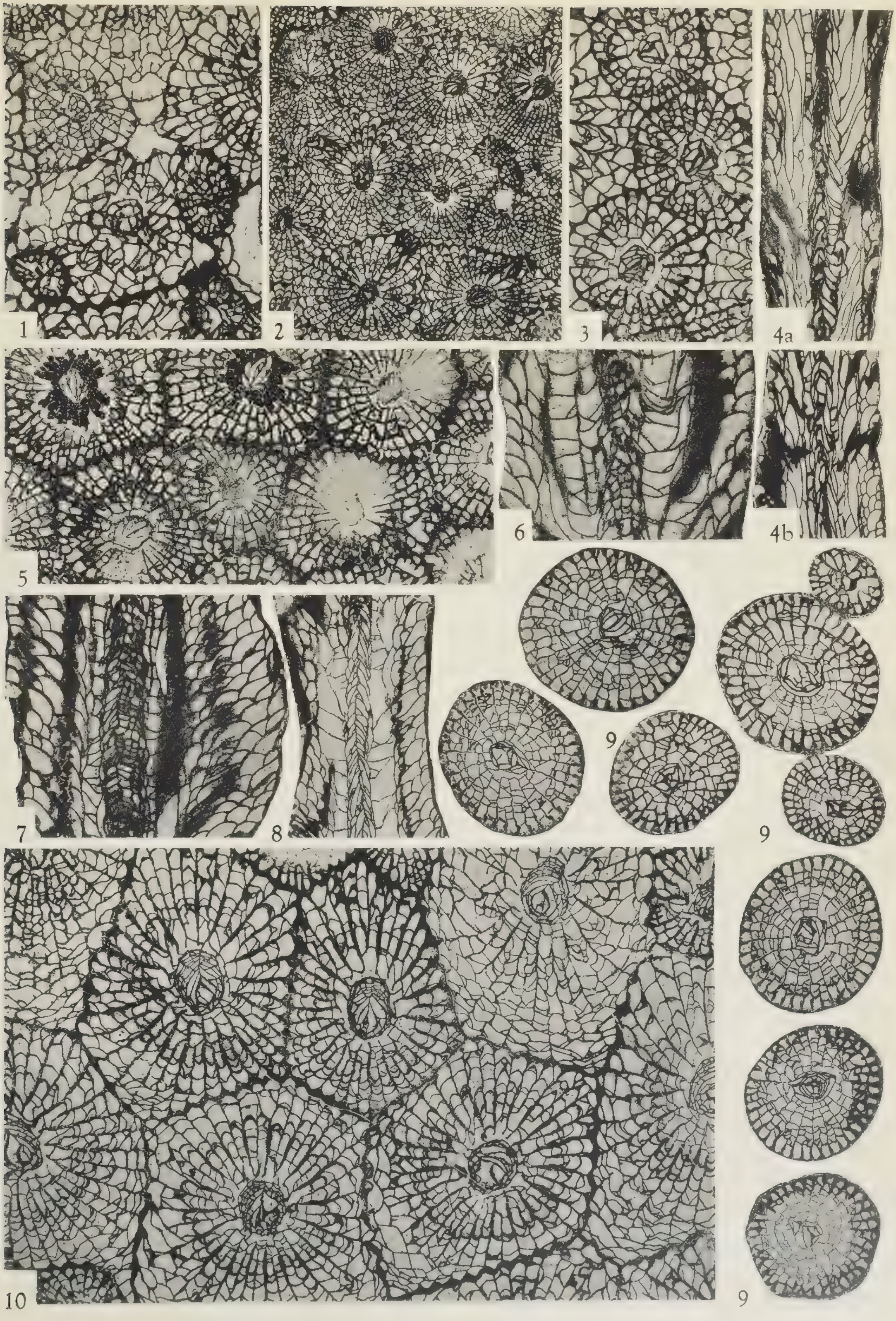
The specimens of figs. 1–3, 5, 7, 8, 10 are from the Wentzelella Limestones, Zinnar Limestone (Permian) of the Harrur section, Chalki, northern Iraq; that of figs, 4, 6, 9 was not *in situ* in the Geli Khana section, Ora, northern Iraq, but was from below the Wentzelella Limestones.

Figs. 1–3, 7, 10. *Ipciphyllum ipci* sp. nov. 1, Trans. sect. R 42019*b* from paratype, ×4·5, showing area of young peripheral corallites and irregular breaking up of parent corallite. 2, Trans. sect. R 42023*a* from paratype, ×2·25. 3, Trans. sect. R 42022*a* from paratype, ×4·5 showing young corallites almost entirely consisting of tabularia. 7, Vert. sect. R 42026*a* from paratype, ×4·5. Note narrow periaxial zone of transverse tabulae; clinotabulae partly obscured by septa. Note evenly sized dissepiments. 10, Trans. sect. R 42028*a* from holotype, ×4·5. Note persistence of fine, irregular medial plate.

Figs. 4, 9. *Waagenophyllum indicum* (Waagen and Wentzel) var. nov. 4*a*, *b*. Vert. sects. from R 42007*a*, ×4·5. Note very irregular septal lamellae and very narrow zone of transverse tabulae. 9, Various trans. sects. from R 42007*b*, ×4·5. Note open axial column attached to counter septum.

Figs. 5, 8. *Ipciphyllum* cf. *subtimoricum* (Huang). 5, Trans. sect. R 42020*a*, ×4·5, partly silicified. Note concentric dissepiments and similarity of major and minor septa. 8, Vert. sect. R 42020*b*, ×4·5. Clinotabulae only show in upper and lower part of figure.

Fig. 6. *Ipciphyllum elegans* (Huang). Vert. sect. R 42001*c*, ×9, not medial through axial column. Note wide tabularium.



HUDSON, Permian corals

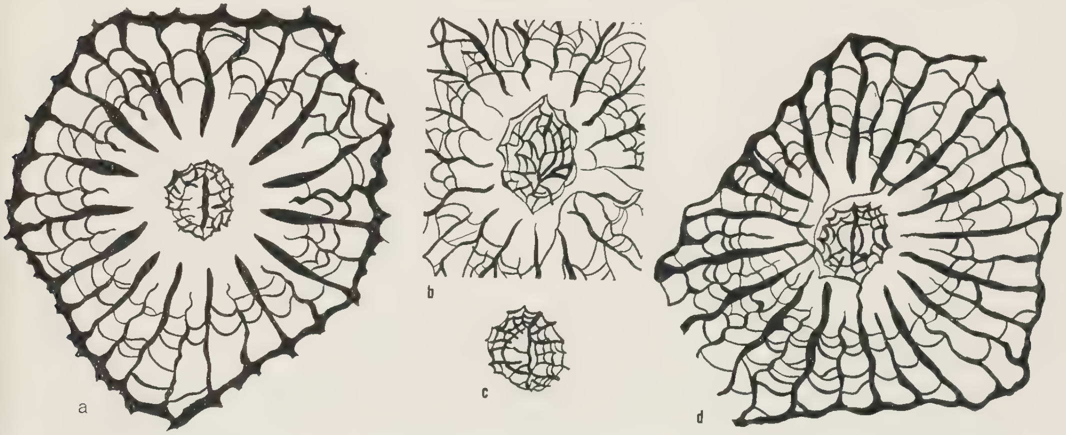
Ipciphyllum elegans (Huang)

Plate 33, fig. 6; text-fig. 1

Wentzelella elegans Huang 1932, p. 61, pl. 4, figs. 3, 4; Douglas 1950, p. 13, pl. 2, fig. 7.

Material. R 42001 (two pieces) and sections *a*, *b* (text-fig. 1), and *c* (Pl. 33, fig. 6). Wentzelella Limestones, Geli Khana section, Ora, northern Iraq.

Description. Cerioid, corallites 5 to 6 mm. across, about thirty-two septa, major thickened within tabularium and extend almost to axial column, minor, flexous and about two-thirds length of major, may fail. Axial column arachnoid, about 1·3 mm. across, thick medial plate, radial lamellae, and few tabellae. Wide tabularium about three-quarters width of corallite, mainly of transverse compound tabulae continuing peripherally into steep simple clinotabulae. Dissepimentarium narrow, dissepiments angulo-concentric. No non-septate dissepimentarium. Quite comparable to type of species.



TEXT-FIG. 1. Transverse sections of axial column of *Ipciphyllum elegans* (Huang), R 42001*b*, ×8·4.

Ipciphyllum cf. *subtimoricum* (Huang)

Plate 33, figs. 5, 8

Cf. *Wentzelella subtimorica* Huang 1932, p. 59, pl. 4.

Material. R 42003 and sections *a*, *b*; R 42005, section *a* only, both from Geli Khana section, Ora; R 42020 (five pieces) and sections *a* (Pl. 33, fig. 5) and *b* (Pl. 33, fig. 8), Harrur section, Chalki. All from Wentzelella Limestones.

Description. Cerioid, corallites about 5 to 6 mm. across, with thirty-six to forty-two septa, major and minor almost equal in length and usually continuous. Axial column up to 1·5 mm. across, of medial plate and tabellae, and rare crestal septal lamellae. Wide tabularium of transverse tabulae and cystose clinotabulae; dissepiments concentric or slightly concave inwards.

Remarks. These specimens, though smaller, are much more similar to the type specimens than most specimens allocated to the species by various authors. The specimen is also very similar to *Ipciphyllum gnomeiense* (Huang) except that that species has non-septal dissepiments.

Ipciphyllym cf. *timoricum* (Gerth)

Text-fig. 4*a*

COMPARE

Lonsdaleia timorica Gerth 1921, p. 74, pl. 145, figs. 1, 2.
Wentzelella timorica Huang 1932, p. 58, pl. 3, figs. 4–6; *non* Heritsch 1937, p. 2, pl. 1, figs. 6*a–d*, 7.
Wentzelella flexuosa Huang 1932, p. 60, pl. 4, fig. 2.

Material. R 42000 (five pieces) and thin sections *a*, *b*, *c* (text-fig. 4*a*), *d*. Wentzelella Limestones, Geli Khana section, Ora.

Though the specimen is not well preserved it shows many of the characteristic features of *Lonsdaleia timorica* Gerth. Both species have a wide axial column of many tabellae, which almost fills the tabularium leaving little room for transverse tabulae: both have a distinct tabularium emphasized by a dissepitheca. The dissepiments of both are curved concentric, but, nevertheless, the Iraq specimen is on a generally smaller scale and often has a peripheral zone of non-septal dissepiments in which respect it is similar to *I. flexuosum* (Huang); it is unfortunate that its bad preservation prevents more precise naming.

'*Lonsdaleia*' *chaoi* Huang var.

Plate 32, figs. 1, 2, 7–9, text-figs. 2, 3*a–e*

Cf. *Stylidophyllum chaoi* Huang in Yoh and Huang 1932, p. 35, pl. 9, figs. 5*a–b* (*? non Stylidophyllum chaoi* Huang 1932, p. 73, pl. 7, fig. 3).
Cf. *Stylidophyllum orientalis* Douglas 1936, p. 16, pl. 3, fig. 3.

Material. Specimen R 41996 (ten pieces) and sections *a–e*. From scree of uppermost bed of Michelinia Limestones, Geli Khana section, Ora, northern Iraq.

Description. Corallum about 23 cm. by 19 cm. by 7 cm. (incomplete), cerioid, with corallites usually six-sided and *c.* 12 mm. across. Calices with shallow, entirely ridged, slopes and an axial area, *c.* 2·5 mm. to 3 mm. across, mainly occupied by axial boss, *c.* 2 mm. across. Epitheca single, with slight crimping corresponding to major and minor septa. Tabularium about half-width of corallite and clearly delineated by thickening of innermost dissepimental surfaces, forming a dissepitheca. Major septa up to twenty-two, thickened within tabularium but with thin, slightly curved or irregular, extensions

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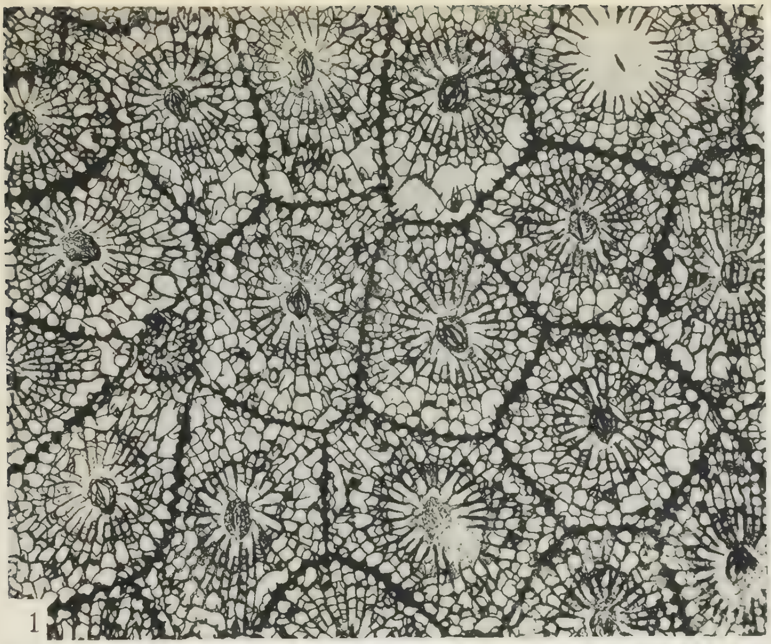
EXPLANATION OF PLATE 34

All figured specimens are from the Wentzelella Limestones, Zinnar Limestone (Permian). Those of figs. 1, 3–5, are from the Harrur section, Chalki, northern Iraq, and those of figs. 2, 6 from the Geli Khana section, Ora, northern Iraq.

Figs. 1, 2, 5, 6. *Wentzellophyllum persicum* (Douglas), ×4·5. 1, Trans. sect. R 42027*c*. Note peripheral non-septal dissepiments. 2, Trans. sect. R 42004*a*. Note tendency to elimination of epitheca. 5, Vert. sect. R 42027*a*, through side and end of axial columns. Note lateral dissepiments, tertiary septa, large non-septal dissepiments and small interseptal dissepiments. 6, Vert. sect. R 42004*b*, through medial plate of axial column.

Figs. 3, 4. *Wentzelella socialis* (Mansuy). 3, Vert. sect. R 42012*b*, ×4·5, through medial plate of axial columns. Note lateral dissepiments flanking septa and tendency to replace septa by dissepisepta. If major and minor septa are followed from axial area, the intercalation of tertiary septa can be noted. 4, Trans. sect. R 42012*a*, × 2·25. Note occasional non-septal dissepiments.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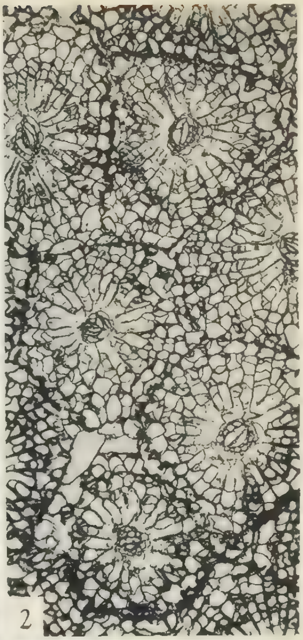
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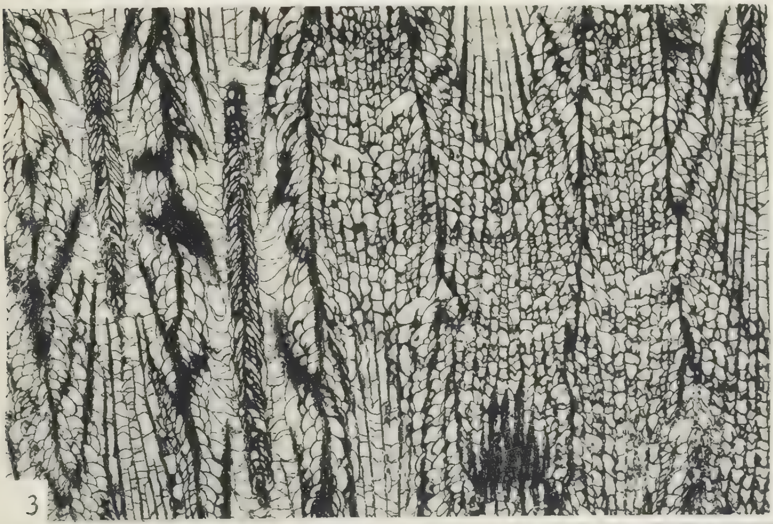
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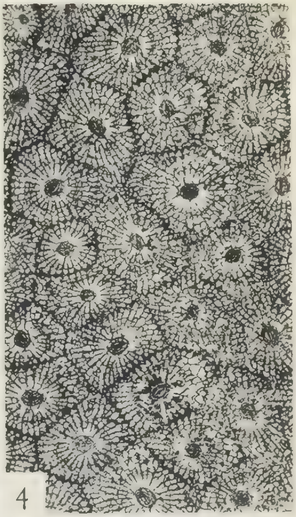
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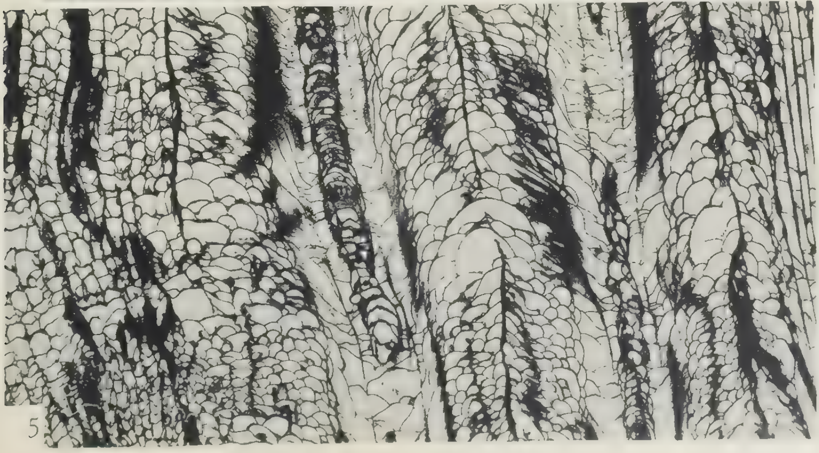
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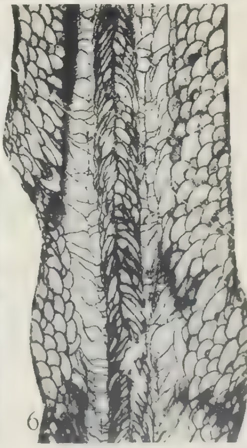
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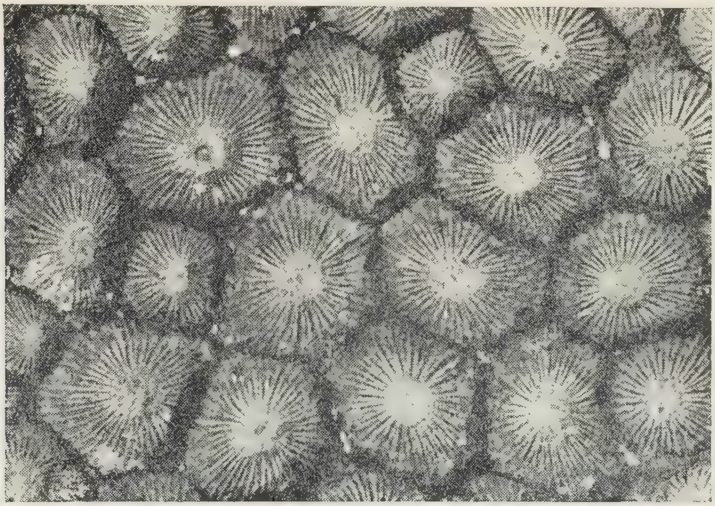
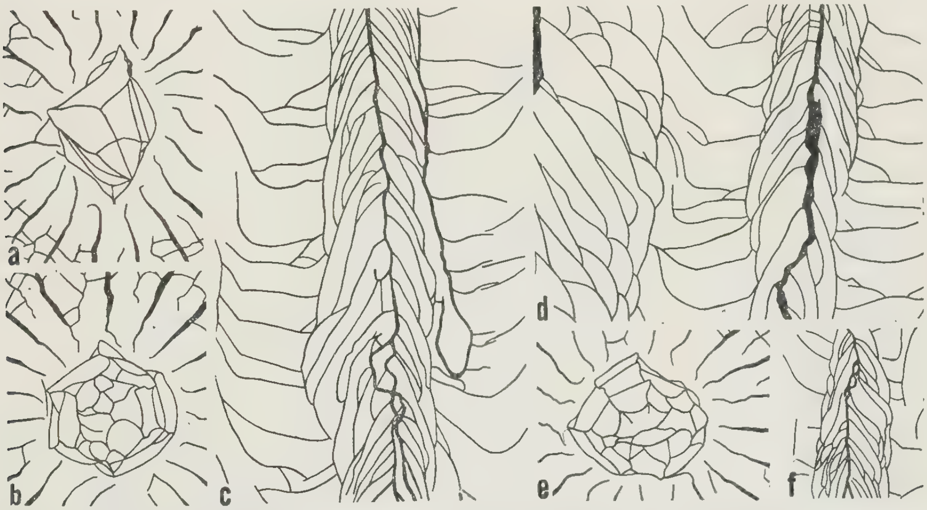


TEXT-FIG. 2. Calicular surface of '*Lonsdaleia*' *chaoi* (Huang) var. × 1·6. Photographed with no side lighting to show continuation of septal ridges across peripheral dissepiments.



TEXT-FIG. 3. *a–e*, '*Lonsdaleia*' *chaoi* (Huang) var.; *a*, *b*, *e*, trans. sect., R 41996*e*, × 8, of axial columns; *c*, *d*, vert. sects., R 41996*d*, × 8, of axial columns. *f*, *Wentzelella canalifera* (Mansuy). Vert. sect., R 42013*a*, × 8·3, of axial column.

reaching almost to axial column; extend, not thickened, about half-way across dissepimentarium but may continue to epitheca or be shorter. Crestal septa absent or feebly developed. Minor septa in tabularium thickened and about half length of major but in dissepimentarium usually extend as far as major. Fossulae absent.

Axial column, when fully developed, circular and *c*. 2 mm. across. Medial plate irregular and often medially thickened, crosses column and, proximally, links with counter and cardinal septa. About six septal lamellae, more or less irregular and radial, may bifurcate. Axial tabellae numerous, about twelve in 5 mm., closely and steeply tented and often entire. Tabulae about nine in 5 mm., horizontal or slightly concave, sharply upturned near dissepimental wall to form clinotabulae, and showing in transverse section a narrow zone of tabular sections entire and curved between septa. Dissepiments shallowly curved and sloping about 45° inwards. Transverse sections of interseptal dissepiments fairly regular though acutely curved, extraseptal dissepiments shallowly curved but irregularly shaped and sized.

Remarks. '*Stylidophyllum*' *chaoi* Huang has an axial column in which the medial plate is not distinct from the other septal lamellae, few in number. Otherwise it does not differ significantly from the Iraq specimen. '*Stylidophyllum*' *orientale* Douglas has up to twenty-six major septa and its axial column, in which the medial plate is thickened along its entire length, is slightly larger and slightly more complex than the majority of those in the Iraq specimen, to which it is otherwise similar. The difference between the above two species and the Iraq specimen is so small that they could be justifiably considered minor varieties of the one species.

WENTZELELLINAE subfam. nov.

Diagnosis. Rugosa, solitary or compound, with septa of three or more orders. Axial column compact, variously of medial plate, tented tabellae, and septal lamellae or crestal septal-lamellae. Inner tabularium of transverse tabulae, outer of clinotabulae which may be near vertical and elongate cystose. Septa may be dissepiseptate or naotic. Peripheral dissepiments may be non-septate or closely crestal-septate.

Remarks. The above definition is based on the morphology of *Wentzelella* widened to include various form-genera which might well be considered subgenera. They include forms in which the dissepimentarium is entirely septate and the corallum solitary (*Iranophyllum* Douglas 1936), phaceloid (? *Heritschiella* Moore and Jeffords 1956), cerioid (*Wentzelella* Grabau 1932), partly cerioid and partly meandroid (*Wentzelloides* Yabe and Minato 1944), mainly thamnasterioid (*Lonsdaleiastraea* Gerth 1921); forms in which the peripheral dissepimentarium is non-septate or crestal septate and the corallum solitary, fasciculate or cerioid (*Wentzellophyllum* gen. nov.), partly cerioid and

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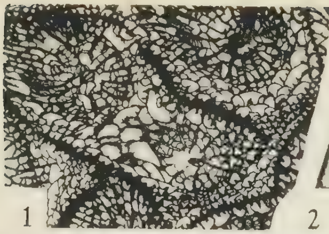
EXPLANATION OF PLATE 35

All figured specimens are from the Wentzelella Limestones, Zinnar Limestone (Permian) of the Harrur section, Chalki, northern Iraq.

Figs. 1, 2, 7. *Polythecalis sp.* cf. *P. japonica* Yabe and Minato. 1, Trans. sect. R 42018*a*, ×2·75. Note extension of tertiary septa from denticles of epitheca. 2, Vert. sect. R 42018*c*, ×5·5, upper part not medial. Note clinotabulae in outer zone of tabularium. Upper part of left dissepimentarium shows beginning of new corallite. 7, Trans. sect. R 42018*b*, ×5·5, with cerioid and aphroid corallites. Note formation of new epitheca around corallite in lower right-hand corner.

Figs. 3, 5, 6, 8. *Wentzelella canalifera* (Mansuy). 3, Vert. sect. R 42014*a*, ×5·5. Middle part of axial column through medial plate. Note interseptal clinotabulae. 5, Vert. sect. R 42013*c*, ×5·5. Left axial column is through side of column showing crestal septal lamellae; right axial column is through end of column. Note zigzag septa. 6, Trans. sect. R 42014*c*, ×2·75. 8, Trans. sect. (slightly oblique) R 42013*b*, ×2·75. Note abnormal non-septal dissepiments associated with breaks in epitheca.

Fig. 4. *Ipciphyllum ipci* sp. nov. Trans. sect. R 42024*b* of paratype, ×2·75. Note various stages in corallite growth.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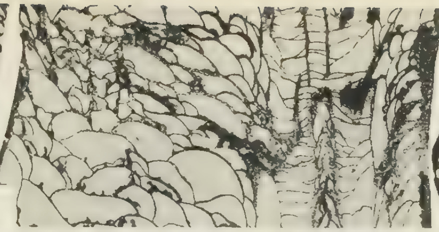
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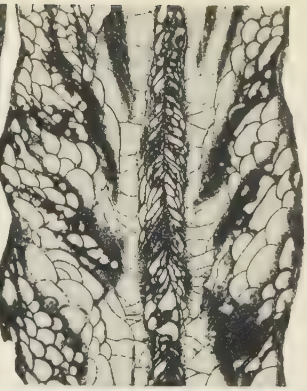
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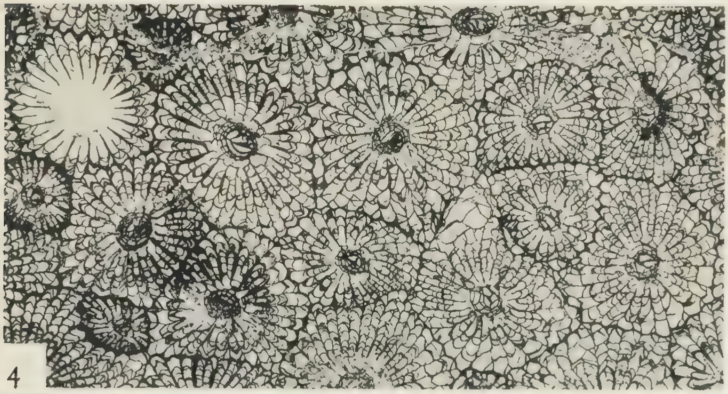
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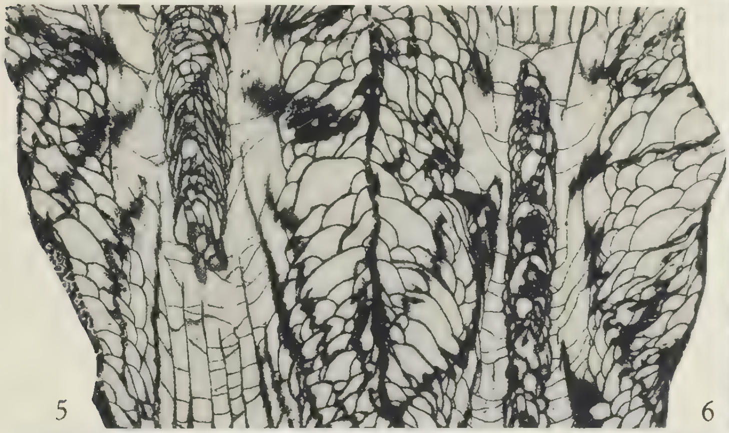
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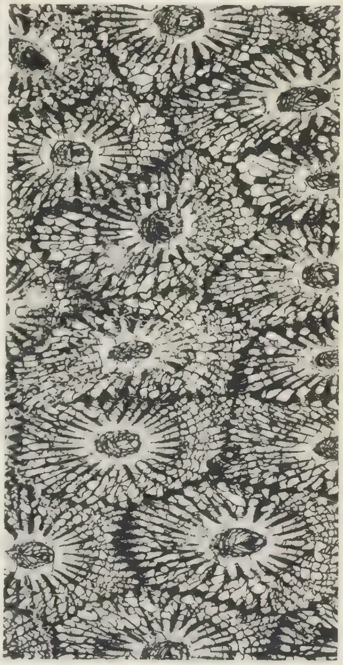
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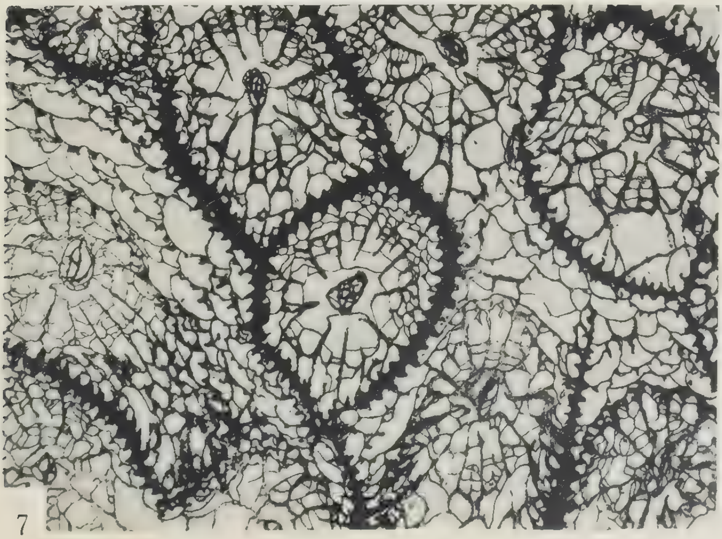
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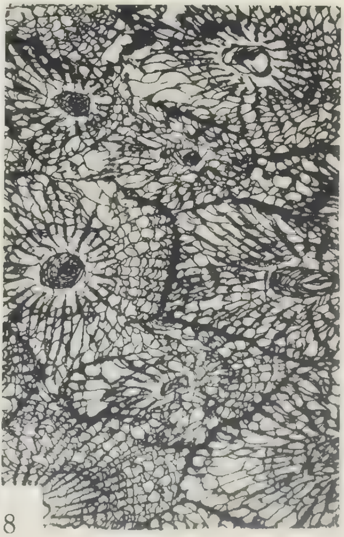
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HUDSON, Permian corals

partly aphroid (*Polythecalis* Yabe and Hayasaka 1916), and almost entirely aphroid (*Cystophora* Yabe and Hayasaka 1916).

WENTZELELLA Grabau *in* Huang 1932

Type species *Lonsdaleia salinaria* Waagen and Wentzel 1886

Wentzelellinae with cerioid corallum, thick epitheca; dissepisepta common, tertiary septa variously developed; dissepimentarium almost entirely septate, lateral dissepiments common; tabulae may be sharply divided into clinotabulae and transverse tabulae (*Wentzelella* is essentially a cerioid *Iranophyllum*).

Wentzelella canalifera (Mansuy)

Plate 35, figs. 3, 5, 6, 8; text-fig. 3*f*

Lonsdaleia canalifera Mansuy 1913, p. 109, pl. 11, fig. 12, pl. 12, figs. 1*a*, *b*, *c*; Sen, 1931, p. 35, pl. 6.
Lonsdaleia molengraffi Gerth 1921, p. 76, pl. 145, figs. 3–5.

Material. R 42014 (nine pieces) and sections *a* (Pl. 35, fig. 3), *b*, and *c* (Pl. 35, fig. 6). R 42013 (five pieces) and sections *a* (text-fig. 3*f*), *b* (Pl. 35, fig. 8), and *c* (Pl. 35, fig. 5). From Wentzelella Limestones, Zinnar Limestone, Harrur section, Chalki, northern Iraq.

Description (Iraq material). Cerioid corallum, thick denticulate epitheca and corallites 5 mm. to 8 mm. across. About thirty-two major and minor septa, thickened in tabularium, minor slightly shorter; tertiary septa sporadically developed, usually in angle of corallite. Axial column, 1·5–2 mm. across, mainly of overlapping tabellae tented against a medial plate, slightly thickened, which may deviate from medial line. Septal lamellae, few, mainly crestal. Tabularium, about half corallite width, of outer steep usually elongate-cystose clinotabulae, and inner simple or compound transverse tabulae. Dissepiments well curved; lateral dissepiments common in peripheral dissepimentarium, which is occasionally non-septate.

Remarks. The above description was based on R 42014. The other specimen has slightly wider corallites and axial columns. Peripheral budding is more common and the growth of neotissue makes the general pattern irregular. The dissepimentarium is also more non-septal and aphroid. The coral thus tends towards *Polythecalis*. The dimensions of these specimens, their septal number and their general pattern are close to those of *W. canalifera*; the small canals between the corallites that occur in the type specimens are, in the opinion of the author, parasitic or symbiotic.

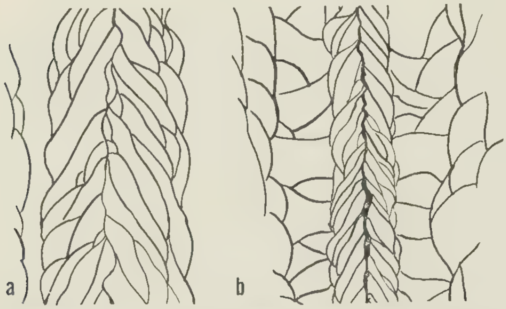
Wentzelella socialis (Mansuy)

Plate 34, figs. 3, 4; text-fig. 4*b*

Lonsdaleia socialis Mansuy 1913, p. 110, pl. 12, fig. 2.

Material. R 42012 (two pieces) and sections *a* (Pl. 34, fig. 4) and *b* (Pl. 34, fig. 3), Harrur Section, Chalki, northern Iraq. R 42015 (seven pieces) and sections *a* (text-fig. 4*b*) and *b*–*g*, Pirispiki section, 1 km. west of Ora, northern Iraq. Both from Wentzelella Limestones, Zinnar Limestone.

Description (Iraq material). Corallites *c.* 5 mm. across. About thirty-two major and minor septa, minor slightly shorter; tertiary septa sporadically developed. Axial column compact, about 0·08 mm. to 0·1 mm. across, mainly closely tented tabulae, short slightly thickened medial plate and few crested radial lamellae. Dissepiments small, well curved, mainly interseptal; lateral dissepiments very common giving a consistent lace-like-pattern in transverse section. Tabularium clearly distinct from dissepimentarium, half to two-thirds width of corallite; clinotabulae not well developed, numerous subhorizontal transverse tabulae. Peripheral dissepimentarium of R 42015 slightly more non-septal.



TEXT-FIG. 4. *a*, *Ipciphyllum* cf. *timoricum* (Gerth), vert. sect., R 42000*c*, ×12; *b*, *Wentzelella socialis* (Mansuy), vert. sect. R 42015*a*, ×12.

Remarks. *Wentzelella canalifera* and *W. socialis* were originally described from the Productus Limestones of Cambodia where they occurred with *Neoschwagerina cratulifera* (Schwager) characteristic of the Neoschwagerina Zone. Sen (1931) records *W. canalifera* from the Middle Productus Limestone of the Salt Range.

WENTZELLOPHYLLUM gen. nov.

Type species. *Lonsdaleia volzi* Yabe and Hayasaka 1915, p. 108; 1920, pl. 8, figs. 6*a*, *b* (see also *Stylidophyllum volzi* (Y. and H.), Huang 1932, p. 65, pl. 6, figs. 1–3, pl. 10, fig. 1; Felser 1937, p. 13, pl. 1, figs. 8*a*, *b*; Heritsch 1939, pl. 2, figs. 6, 18).

Diagnosis. Wentzelellinae, with denticulate epitheca, and dissepimentarium with peripheral zone with, all or in part, no septa or crestal septa.

Remarks. The genus is founded to include those Lonsdaleoid corals with tertiary septa and clinotabulae that have previously been included in the genus *Stylidophyllum* de Fromental 1861 (type species *Lonsdaleia floriformis* Martin, which has neither tertiary septa or clinotabulae). Though most of the species so included are cerioid forms, the genus is so founded that solitary or fasciculate corals are included.

Wentzellophyllum persicum (Douglas)

Plate 34, figs. 1, 2, 5, 6

Wentzelella persica Douglas 1936, p. 24, pl. 2, fig. 3.
Cf. *Stylidophyllum gnomeiense* Huang 1932, p. 75, pl. 7, fig. 2; Heritsch 1939, p. 176, pl. 1, figs. 4, 5; pl. 2, figs. 11, 12.

Material. R 42004 (six pieces) and sections *a* (Pl. 34, fig. 2) and *b* (Pl. 34, fig. 6) from Geli Khana section, Ora, northern Iraq. R 42025 (five pieces) and sections *a*, *b*, *c*; R 42027 (seven pieces) and sections *a* (Pl. 34, fig. 5), *b*, *c* (Pl. 34, fig. 1), both from Harrur section, Chalki, northern Iraq. All from Wentzelella Limestones, Zinnar Limestone.

Description (Iraq material). Corallites polygonal, from 6 to 7 mm. across, epitheca occasionally absent. Usually thirty septa, thickened in tabularium, minor slightly shorter.

Sporadic development of short tertiary crestal septa. Axial column mainly of medial plate not thickened and numerous axial tabellae, septal lamellae short and crestal; transverse section of column about 0·1 mm. by 0·08 mm. across. Tabularium about one-third of corallite width, with clinotabulae and transverse tabulae. Dissepiments usually small and hemispherical; non-septal dissepiments strongly convex inwards, sides of dissepiment continue line of septa.

Remarks. The specimen figured on Pl. 34, fig. 1 is similar to that figured by Douglas; R 42025 and that on Pl. 34, fig. 2 is slightly more irregular and dissepiments are not so markedly non-septal. The general morphology is similar to that of *Wentzelella socialis* (Mansuy) of which it could be considered the Lonsdaleoid representative. '*Stylidophyllum*' *gnomeiense* Huang and especially that figured by Heritsch from the neighbouring area in Anatolia are comparable to *Wentzellophyllum persicum*; they have perhaps a few additional septa.

POLYTHECALIS Yabe and Hayasaka *emend.* Tseng

Type species *Polythecalis confluens* Yabe and Hayasaka 1916

Wentzelellinae with corallum, partly cerioid and partly aphroid, with thick denticulate epitheca; peripheral dissepimentarium mainly non-septal or crestal-septate. Clinotabulae may be simple, compound, or cystose, and transverse tabulae variously developed.

Polythecalis sp. cf. *P. japonica* Yabe and Minato

Plate 35, figs. 1, 2, 7

Cf. *Polythecalis japonica* Yabe and Minato 1946, p. 466, figs. 1–3; Minato 1955, p. 132, pl. 32, fig. 1 as *Stylidophyllum sikokuense* Minato nom. nov.
Cf. *Stylidophyllum arminae* Felser 1937, p. 14, pl. 1, figs. 9*a*–*c*.
COMPARE ALSO
Aphroid forms: *Polythecalis rosiformis* Huang *in* Yoh and Huang 1932, p. 42, pl. 10, figs. 1*a*–*c*; Heritsch 1939, p. 175, pl. 1, figs. 1, 6–8.
Lonsdaleoid forms: *Stylidophyllum variabile* var. *a* and *b*, Gerth 1938, p. 233, pl. 15, figs. 2–6.
Meandroid forms: *Wentzelelloides maiyaensis* Yabe and Minato 1944, p. 141, pl. 12; Minato 1955, p. 114, pl. 24.

Material. R 42018 (three pieces) and sections *a* (Pl. 35, fig. 1), *b* (Pl. 35, fig. 7), and *c* (Pl. 35, fig. 2). From Wentzelella Limestones, Harrur section, Chalki, northern Iraq.

Description. (Iraq material). Fragment of cerioid and aphroid corallum. Cerioid corallites, 5 to 6 mm. across, some almost circular, but usually polygonal with four or five curved sides. Epitheca *c.* 0·3 mm. thick with denticles, up to sixty in a corallite, usually opposite and irregularly corresponding to septa of various orders. When cerioid, corallite consists of a tabularium *c.* 3 mm. across, with an irregular dissepitheca and a narrow though variable dissepimentarium. When aphroid, the tabularium is irregular and not clearly defined and the dissepimentarium is very variable in width. Major septa ten to fourteen (usually ten), extend from dissepitheca almost to axial column (the counter may be slightly longer and the cardinal shorter than the others). Minor septa generally about one-third the major but may be little more than ridges on the dissepitheca. Both major and minor thickened within tabularium; both extend into the dissepimentarium as thick discontinuous crestal septa which may be closely aligned forming a secondary epitheca. In some aphroid corallites the septa edging the epitheca may be more continuous. Third and occasional fourth-order septa exist as short extensions of the denticles.

Axial column oval, *c.* 0·5 by 0·8 mm. or less, with an irregular medial plate, a few lateral axial tabellae (usually one or two on each side), and a few crestal septal lamellae. Inner tabularium of horizontal or steeply inwardly compound tabulae; outer tabularium of large vertically elongated clinotabulae. Transverse tabular sections very irregular. Dissepiments steeply convex upwards and very variable in size. Lateral dissepiments occur abundantly flanking or even replacing the crestal septa, and thus forming dissepisepta.

Remarks. The various species listed above have a very similar septal pattern. The major septa are few, the minor septa are very irregularly developed and there are various tertiary septa. The axial column is dominated by tabellae and the septal lamellae are usually crestal and few. In each species the budding is peripheral, usually paired and with incomplete fission. Apart from the method of linking one corallite to the other the differences between the species are slight and are mainly differences in corallite width, in number of septa and septal lamellae. These species, however, do show different stages in the elimination of the epitheca and have, therefore, been variously allocated to the form genera *Wentzelella* (cerioid), *Wentzelloides* (meandroid), *Wentzellophyllum* (lonsdaleoid), and *Polythecalis* (part or entirely aphroid), genera most of which show one or more of these trend stages. The Iraq specimen is most like *Polythecalis japonica* from the Polythecalis Zone of Japan. It is, however, also closely similar to '*Stylidophyllum*' *arminae* Felser from the Karnic Alps which has, however, more regular dissepiments. The specimen figured by Felser as pl. 1, fig. 9 suggests that this species is also partly aphroid and it may be a synonym of *P. japonica*. Another possible synonym is '*Stylidophyllum*' *variabile* var. *a* Gerth from the Permian of the eastern Caracorum of the Himalayas. The corallum is cerioid with polygonal corallites, mostly straight-sided, occasionally linked the one with the other by the weakening or suppression of the epitheca, which is normally very thick. The dissepimentarium is either entirely septate or closely laced with crestal septa; the dissepiments are therefore small and vary little in size. Its septal plan and the pattern of its tabularium and dissepimentarium are otherwise very similar to those of *P. japonica* which, however, is slightly more aphroid. '*S.*' *variabile* var. *b* Gerth is like the section of the Iraq specimen figured as Pl. 35, fig. 1. Gerth's varieties *a* and *b* are probably, as he suggests, different growth stages in the one form.

Of the forms described from neighbouring areas, those most like the Iraq specimen are *Polythecalis rosiformis* Huang as figured by Douglas from Iran and by Heritsch from Anatolia. These forms are more aphroid and have a smaller and more regular tabularium which may consist entirely of clinotabulae.

Order TABULATA Milne-Edwards and Haime

Michelinia favositoides Girty

Plate 32, figs. 5, 6

Michelinia favositoides Girty 1908, p. 38; 1913, p. 312, pl. 29, figs. 1–2 (*non Michelinia favosoidea* Billings 1859, p. 114).

Cf. *Michelinia* (*Protomichelinia*) *microstoma* Yabe and Hayasaka 1915, p. 61; Yabe and Hayasaka 1920, pl. 9, figs. 8*a*–*b*.
Cf. *Michelinia microstoma* Huang 1932, p. 92, figs. 3*a*, 3*b*.
Cf. *Michelinia mansuyi* Reed 1925, p. 12, pl. 1, figs. 16–21.
Cf. *Michelinia* (*Michelinopora*) *multitabulata* Yabe and Hayasaka 1915, p. 59.
Cf. *Michelinia* (*Protomichelinia*) *multitabulata*, Minato 1955, pl. 26, figs. 1, 2, pl. 31, fig. 2.
Cf. *Michelinia siyangensis* Heritsch 1939, pl. 2, fig. 3 (*non Michelinia siyangensis* Reed 1927, p. 108, pl. 7, figs. 4, 5).

Material. R 41997 (three pieces) and sections *a* (Pl. 32, fig. 5) and *b* (Pl. 32, fig. 6) and R 41999 (two pieces) both from Michelinia Limestones, Geli Khana section, Ora, northern Iraq. R 42055 (two pieces) from Michelinia Limestones, Chia-i-Zinnar, Chalki, northern Iraq.

Description (Iraq material). Corallum hemispherical (R 41997 about 5 cm. across and 3·5 cm. high). Holotheca not known. Full-grown corallites usually six-sided and generally 1·5 mm. (max. 2 mm.) across. Corallite walls about 0·2 mm. thick with a medial dark strand and flanked by tissue of spine bases. Numerous approximately circular pores about 0·2 mm. across and fairly evenly distributed (about 0·3 to 0·5 mm. apart). Septal spines, short but distinct, and generally equal, about twenty to twenty-five in a corallite transverse section. They are arranged in vertical rows on the inner surface of the epitheca, each row separated by a very fine groove, thus forming vertical septal ridges well evident in weathered corallites. Tabulae very thin, slightly curved with convex surface upwards, some flat; many short and incomplete, abutting on tabula below; approximately equally spaced, about 10 in 5 mm.

Remarks. The specimen, now known to be from the Chihsia Limestone of China, described by Girty (1908, 1913) as *Michelinia favositoides*, is in all ascertainable features identical with the Iraq specimens. Similar forms are *Michelinia microstoma* Y. and H. also from the Chihsia Limestone and *M. mansuyi* Reed from the Pamir Range. Though these differ slightly from *M. favositoides* (*M. microstoma* has slightly wider corallites and indistinct septal spines; *M. mansuyi* also has wider corallites and also much closer tabulae) they were considered by both Yabe and Hayasaka (1915) and by Huang (1932) to be the same as that species (Yabe and Hayasaka 1915, under the mistaken impression that *Michelinia favositoides* Girty was a homonym of *Michelinia favosoidea* Billings 1859, considered it to be an invalid name and, again mistakenly, replaced it by *Michelinia microstoma* (Y. and H.). Another comparable form, from the lower part of the Chihsia Limestone, is *Michelinia multitabulata* Y. and H. As figured by Minato it differs from *M. favositoides* only in that the septal spines are indistinct and the corallites are generally wider (3 to 4 mm. across). Forms figured as *Favosites* from the Permian (as *P. relicta* Gerth 1921, Heritsch 1934, and *Favosites sp.* Hill 1942) have similarities to *M. favositoides* but it has not been possible to make close comparison. The *Michelina* figured by Heritsch in his description of the Anatolia fauna has marked septal spines and tabulae spaced at nine to ten in 5 mm. Though the width of its corallites, generally about 3 mm. across, is greater than that of *M. favositoides* it should be compared with that species rather than with *M. siyangensis*. It is therefore the opinion of the author that the various forms listed above, and probably others from the lower part of the Permian limestone of Tethys, should be allocated to *M. favositoides* Girty or local varieties of that species.

Michelinia sp. cf. *M. siyangensis* Reed

Plate 32, figs. 3, 4

Cf. *Michelinia siyangensis* Reed 1927, p. 108, pl. 7, figs. 4, 5; Huang 1932, p. 94, pl. 12, figs. 1–6; Douglas 1936, p. 26, pl. 3, figs. 10, 10*a*.

Cf. *Michelinia* cf. *placenta* Yoh and Huang 1932, p. 22, pl. 6, figs. 1, 2 (*non Michelinia placenta* Waagen and Wentzel 1886, p. 852, text-figs. 2*a–d*).

Material. R 41998 (two pieces) and sections *a* (Pl. 32, fig. 4) and *b* (Pl. 32, fig. 3). From Michelinia Limestones, Geli Khana section, Ora, northern Iraq.

Description (Iraq material). Corallum hemispherical, about 2·5 cm. across. Corallites polygonal, *c.* 2 to 2·5 mm. across. Epitheca *c.* 0·2 mm. thick. Pores large and irregularly spaced. Septal spines generally indistinct. Tabulae thin, about 1 mm. apart, generally entire.

Remarks. Only a fragment of this form has been collected. It is distinguished from *M. favositoides* by its wider corallites, lack of marked septal spines, and wider spacing of its tabulae. Since the forms figured by Yoh and Huang as *M.* cf. *placenta* and by Reed, Huang, and Douglas as *M. siyangensis* have wider corallites (up to 4 mm. across), the Iraq specimen is not definitely referred to that species.

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THE SCAPULA OF *PLIOSAURUS MACROMERUS* PHILLIPS

by L. B. TARLO

ABSTRACT. The scapula of *Pliosaurus macromerus* from the Kimeridge Clay (Jurassic) is described for the first time. It differs in shape from the scapulae of all other Plesiosaurians by the anterior production of its dorsal process. This change in shape and the consequent increase in the pre-glenoid length of the pectoral girdle confers important functional advantages which are outlined. The locomotion of Pliosaurs is briefly considered, and it is suggested that the main propulsive force was from the hind limbs.

IN 1952 the post-cranial skeleton of a giant specimen of *Pliosaurus macromerus* Phillips was uncovered at the village of Stretham, near Ely, during excavations of Kimeridge Clay by the Great Ouse River Board. It is housed in the Sedgwick Museum, Cambridge (J. 35990). This specimen is the only Kimeridgian Pliosaur in which limb girdles are known associated with the axial skeleton, and the scapula is of particular interest as it is quite unlike that of any other type of Pliosaur, or indeed of any other reptile.

Several isolated Pliosaur scapulae of Kimeridgian age have previously been recorded, but they are similar to scapulae known from the Oxford Clay. Lydekker (1889, p. 122) figured an immature scapula from the Kimeridge Clay and listed (p. 126) an adult one which I now figure (text-fig. 1*b*; Pl. 36, figs. 1, 1*a*).

This type of scapula is a triradiate bone with a strong thickened glenoid ramus which bears a facet for the articulation of the coracoid, and another which forms the anterior part of the glenoid cavity. Medially the scapula thins out and is expanded into a broad flat sheet termed the ventral plate. Laterally there is a further extension—the dorsal process which is approximately the same width as the glenoid ramus, but again forms a thin sheet. The dorsal process projects either laterally or posterolaterally and in ventral view is set off at an angle to the plane of the bone from a ridge which extends to the anterior point of the ventral plate from the glenoid cavity (Pl. 36, fig. 1*a*).

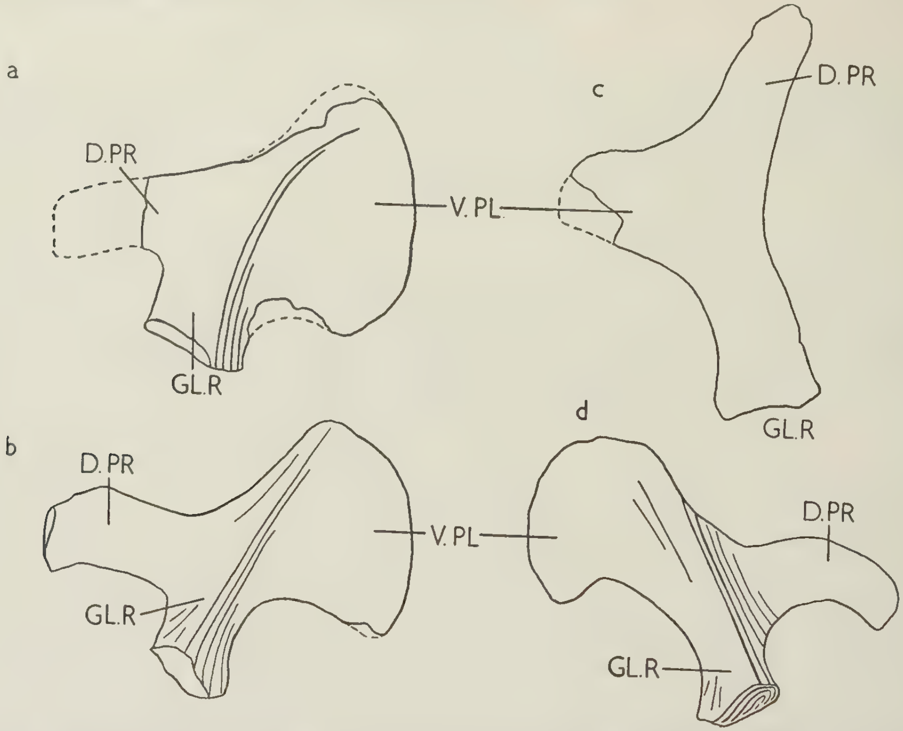
The three scapulae *Peloneustes philarchus* from the Oxfordian, *Pliosaurus sp*. from the Kimeridgian and *Kronosaurus queenlandicus* from the Lower Cretaceous (text-fig. 1) form a reasonable morphological series in which the ventral plate is progressively expanded and the dorsal process moves forward. The scapula of *Pliosaurus macromerus* (text-fig. 1*c*) obviously cannot be included in any such morphological series. It is again a triradiate bone, but it has quite a different shape from the scapulae I have mentioned previously. Again, one process is thickened and this I take to be the glenoid ramus, although unfortunately its end is crushed and it is not possible to recognize the two facets normally present. This time the surface of the bone is in one plane, no part of it being set off at an angle.

I consider that the narrow elongated projection, rather than the broad flange, must be the dorsal process, despite its position relative to the glenoid, i.e. produced anteriorly instead of laterally. This process could not have formed the ventral plate as it would have produced a very weak connexion in the mid-line, which is unlikely in an animal

[Palaeontology, Vol. 1, Part 3, 1957, pp. 193–9. pls. 36–37.]

nearly 40 feet in length. This leaves the third process to be the ventral plate, although its expansion is less marked than, for example, in *Peloneustes philarchus*.

The dorsal process is increased in size, and by virtue of its elongation anteriorly, considerably increases the pre-glenoid length of the whole pectoral girdle (see text-fig. 2). Watson (1924) suggested that in Pliosaurs the dorsal process at no time moved forward, but here we have a striking case of its not only moving forward, but moving much farther forward than in any other Plesiosaurian.



TEXT-FIG. 1. Scapulae in ventral view. *a*, *Kronosaurus queenlandicus* Longman, right scapula, Lower Cretaceous. Mus. Comp. Zool. Harvard 1285. Figured by White 1940, fig. 11*a*. $\times\frac{1}{13}$. *b*, *Pliosaurus sp.*, right scapula, Kimeridgian. B.M. (N.H.) R. 287. Listed by Lydekker 1889, p. 126. $\times\frac{1}{10}$. *c*, *Pliosaurus macromerus* Phillips, left scapula, Kimeridgian. Sedgk. Mus. J. 35990. $\times\frac{1}{8}$. *d*, *Peloneustes philarchus* (Seeley), left scapula, Oxfordian. B.M. (N.H.) R. 3318. Figured by Andrews 1913, fig. 21. $\times\frac{1}{5}$. D. PR., dorsal process; GL. R., glenoid ramus; V. PL., ventral plate.

Taking the girdle as a whole, the large flat coracoids would have met in the mid-line

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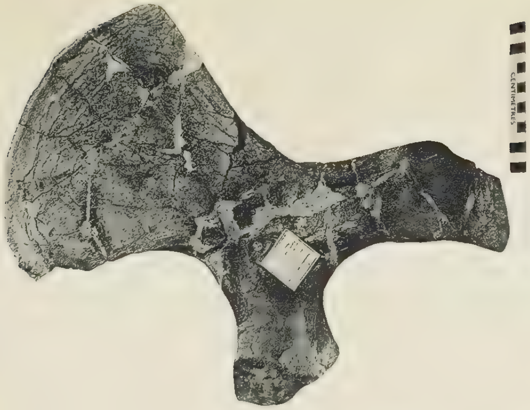
EXPLANATION OF PLATE 36

Figs. 1. 1*a*. *Pliosaurus sp.*, right scapula, Kimeridge Clay, Shotover, near Oxford. 1, dorsal view. 1*a*, ventral view. Brit. Mus. (N.H.) R 287.

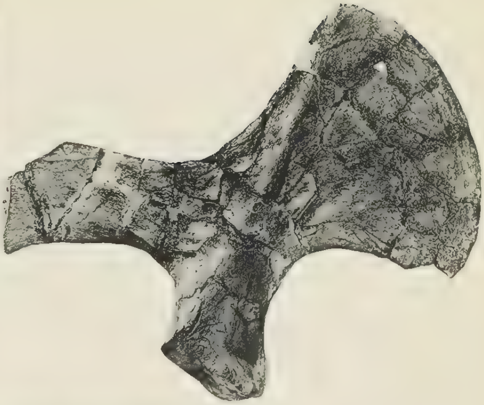
Figs. 2. 2*a*. *Pliosaurus macromerus* Phillips, left scapula, Kimeridge Clay, Ely. 2, ventral view. 2*a*, dorsal view. Sedgk. Mus. Cambridge J. 46. 911.

Figs. 3. 3*a*. *P. macromerus*, right scapula, Kimeridge Clay, Shotover. 3, dorsal view. 3*a*, ventral view. Univ. Mus. Oxford. J. 10. 459.

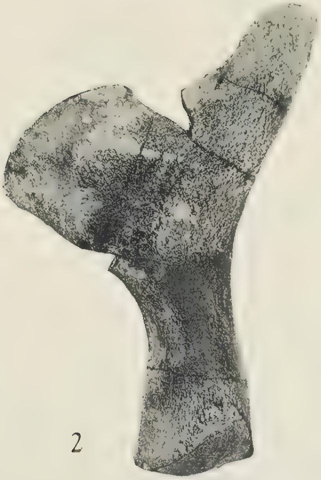
Fig. 4. *P. macromerus*, right scapula, Kimeridge Clay, Coppock's Pit, Shotover. Ventral view. Manchester Museum. 3175.



1



1a



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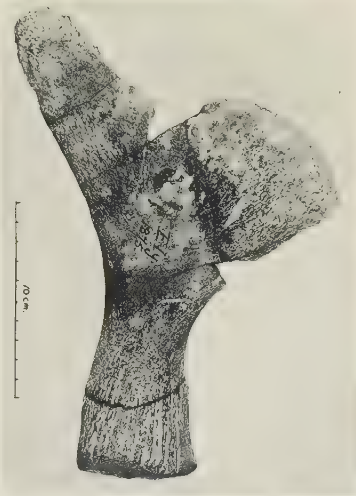
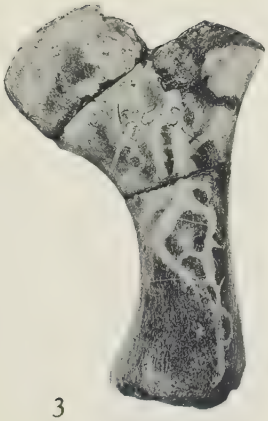
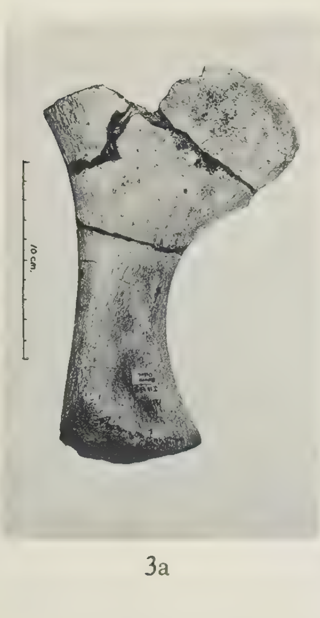


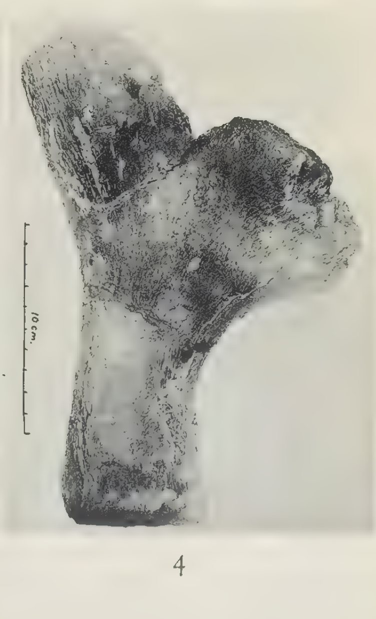
2a



3



3a

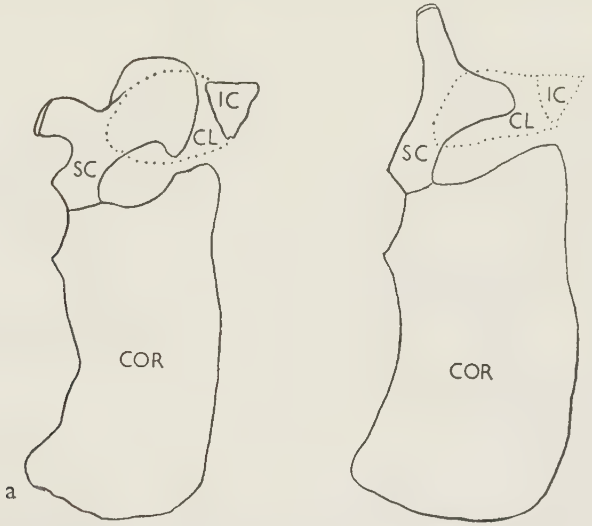


4

TARLO, Jurassic *Pliosaurus*

at an angle, as is indicated by the bevelling of their symphysial surfaces. This suggests that in the anterior part of the girdle the scapulae would also have been held at a similar angle. The ventral plates of the scapulae are not large enough to meet in the mid-line and on their medial edges there is no indication of a cartilaginous extension which might have joined them. My conjecture is that the ventral plates of the scapulae were firmly united by a clavicular arch consisting of an interclavicle and two clavicles, rather like that suggested for *Peloneustes philarchus* by Andrews (1913).

The existence of two distinct types of scapula and consequently two distinct types of pectoral girdle within the Kimeridgian Pliosaurs leads one to believe that there were at least two phylogenetic lineages present in Kimeridgian times. *Kronosaurus* from the Lower Cretaceous may represent the continuation of the more conservative type.



TEXT-FIG. 2. Pectoral girdles in dorsal view. *a*, *Peloneustes philarchus* (Seeley), × $\frac{1}{9}$, from Andrews. *b*, *Pliosaurus macromerus* Phillips, × $\frac{1}{16}$. CL., Clavicle; COR., Coracoid; IC., Interclavicle; SC., Scapula. Dotted lines indicate possible position of clavicular arch.

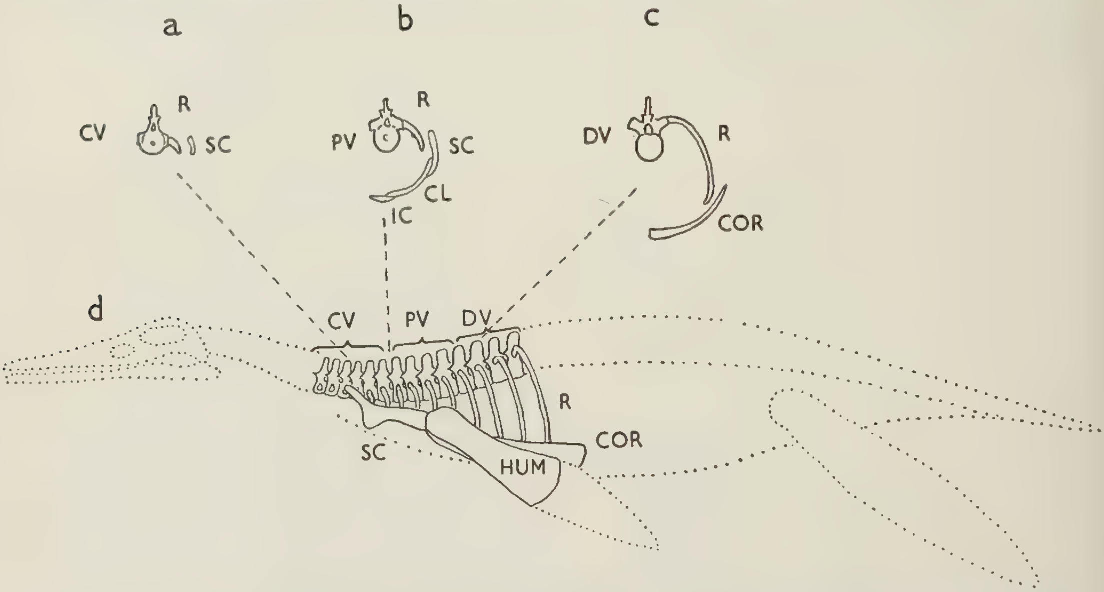
It is worth noting that the remarkable scapula from Stretham is not unique. Since seeing it I have recognized several similar scapulae. An extremely well-preserved left scapula of this type belonging to an immature animal is housed in the Sedgwick Museum, Cambridge (Pl. 36, figs. 2, 2*a*). This is from the Kimeridge Clay of Ely. An examination of this bone confirms that the thickened end of the Stretham scapula is indeed the glenoid ramus, as in this case articular facets for both coracoid and humerus are present.

The Oxford University Museum have an immature right scapula, the dorsal process of which has been broken off, but a comparison with the Ely specimen clearly establishes its identity (Pl. 36, figs. 3, 3*a*). In addition there are two specimens in the Manchester Museum—a right and a left scapula, the larger and more complete of which is shown in Pl. 36, fig. 4. This specimen is from the Kimeridge Clay of Coppock's Pit, Shotover.

These scapulae are isolated specimens, and thus it has not hitherto been possible to identify them. The discovery of the associated skeleton at Stretham in 1952 now allows them to be assigned provisionally to the species *Pliosaurus macromerus*.

As this unusual type of scapula has not previously been noted it is important to investigate the significance of its peculiar shape. In text-fig. 3 I have indicated the position of the bone in relation to the rest of the thorax, and have shown how the anterior production of its dorsal process means that the scapula extends well forward. The musculature of the pectoral girdle must therefore be examined to see in what way it has been affected by this change.

The Stretham scapula shows roughened areas which indicate the position of the insertions or origins of muscles. These are clearly visible in Pl. 37, figs. 1, 1*a*. Text-fig. 4 shows diagrammatically the important muscles of the pectoral girdle, but in this section I shall be concerned only with those related to the scapula.



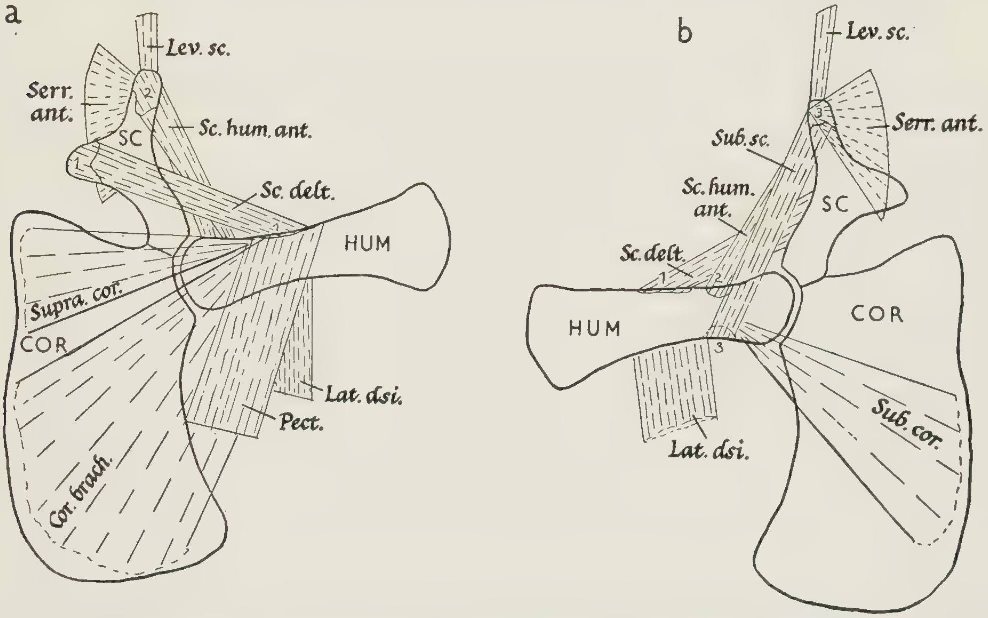
TEXT-FIG. 3. Diagram showing probable position of scapula of Stretham Pliosaur in the body. *a*, transverse section through posterior part of neck and dorsal process of scapula. *b*, transverse section through anterior part of thorax and clavicular arch. *c*, transverse section through posterior part of thorax and coracoid. *d*, lateral view of thorax and pectoral girdle. CL., Clavicle; COR., Coracoid; HUM., Humerus; IC., Interclavicle; R., Rib; SC., Scapula; V., Vertebrae (CV., cervical; PV., pectoral; DV., dorsal).

On the ventral surface of the ventral plate of the scapula is a large roughened area for the origin of the scapular deltoid muscle, which is inserted on the anterior surface of the proximal end of the shaft of the humerus. At the end of a swimming stroke the anterior edge of the humerus faces downwards, and is then rotated into the horizontal plane by this muscle, which also draws the limb forward so that it offers the least resistance to the water.

The scapulohumeralis anterior muscle originates on the distal part of the ventral (external) surface of the dorsal process. It is inserted on the anterior edge of the dorsal surface of the proximal end of the humerus. This muscle also draws the humerus forwards, but at the same time lifts it and rotates its anterior edge upwards.

The origin of the subscapularis muscle is on the distal part of the dorsal (visceral) surface of the dorsal process, and its insertion is on the posterior part of the dorsal surface of the shaft of the humerus, behind the scapulohumeralis anterior. The action of this muscle is to draw the humerus forwards and lift it while rotating its anterior edge downwards.

These two muscles, the scapulohumeralis anterior and the subscapularis, act in concert and are thus able to determine at what angle the forelimb is held as it is drawn forwards. For example, if the subscapularis is contracted more than the scapulohumeralis anterior, the anterior edge of the forelimb is depressed and a backing stroke results. By backing with one forelimb and swimming with the other, the animal is able to turn rapidly.



TEXT-FIG. 4. Diagrammatic reconstruction of pectoral girdle of Stretham Pliosaur. $\times\frac{1}{16}$. *a*, Ventral view; *b*, Dorsal view. COR., Coracoid; HUM., Humerus; SC., Scapula. Muscles: *cor. brach.*, coracobrachialia; *lat. dsi.*, latissimus dorsi; *lev. sc.*, levator scapulae; *pect.*, pectoralis; *sc. delt.* (1), scapular deltoid; *sc. hum. ant.* (2), scapulo-humeralis anterior; *serr. ant.*, serratus anterior; *sub. cor.*, subcoracoideus; *sub. sc.* (3), subscapularis; *supra. cor.*, supracoracoideus. Nos. 1, 2, 3 indicate insertions or origins.

The large roughened area extending forward from the glenoid end of the scapula probably marks the place of attachment of the capsular ligament which holds the head of the humerus in the glenoid cavity. The distal end of the dorsal process has a pitted surface indicating that it is capped by cartilage, and in all probability the levator scapulae muscle is inserted on it. This muscle originates on the back of the skull and holds the pectoral girdle firm, preventing it from slipping backwards during any forward movement of the humerus. On the visceral surface of the dorsal process is the origin of the serratus anterior muscle, which is inserted on to a number of ribs. This forms a sling which prevents any rotation of the girdle around the ribs when the forelimb is moved in a vertical direction, as occurs during swimming, diving, and rolling.

From the foregoing it can be seen that the anterior production of the dorsal process has affected two groups of muscles: (i) those concerned with holding the girdle firm (levator scapulae and serratus anterior), and (ii) those concerned with drawing the humerus forward (scapulohumeralis anterior and subscapularis). In both cases the attachments of these muscles are carried far forward. It seems reasonable to suppose that as a result the levator scapulae muscle is shortened and the girdle is more rigidly held. It also means that the dorsal process to which the serratus anterior muscle is attached now projects forward into the posterior part of the neck where the ribs are very short. In this way the 'sling musculature' is shortened and thus becomes firmer, allowing very little play—an obvious advantage to a giant animal that has to dive in pursuit of its prey.

The more anterior origin of the 'backing' muscles (scapulohumeralis anterior and subscapularis) increases their length, thereby extending the distance through which they can contract. The forelimb can thus be drawn forward through a greater arc and can also be lifted higher, allowing a longer and more powerful swimming stroke. Besides this, these muscles now pull at a greater angle to the humerus, so that less force is required to move it.

The shape of the Stretham Pliosaur scapula therefore seems to be due to the functional advantages which changes in the various muscle insertions confer. *Pliosaurus macromerus* thus appears to be a more efficient swimming and diving animal than its Oxfordian ancestors or the conservative contemporaneous forms.

NOTE ON THE LOCOMOTION OF PLIOSAURS

It has generally been considered that Pliosaurs swam by rowing themselves through the water with their limbs acting as paddles, but I have come to the conclusion that it is more likely that Pliosaurs in fact swam with their hind limbs providing the main propulsive force, while their forelimbs performed a strong forward swimming stroke or initiated a change in direction.

In his paper on the Liassic Plesiosaurian *Plesiosaurus guilelmi imperatoris* Dames (1895) figured a skeleton (part of which I reproduce as Pl. 37, fig. 2) which shows the impression of an extension of skin along the posterior edge of the right forelimb. This means that in section the limb would taper posteriorly, producing a hydrofoil and not the ellipse of an oar, and it is unlikely that the later more streamlined Pliosaurs would have lost such an important feature.

The most effective swimming stroke is one in which the forelimb is driven downwards through the water with its dorsal surface facing forwards and slightly upwards, from a position in which the limb is somewhat above the horizontal and a little forward from the glenoid. This action with a hydrofoil-shaped limb creates less turbulence than does the stroke of an oar, and consequently is more efficient.

With this swimming stroke, the pressure of water is less on the dorsal surface of the limb than on the ventral side, and there is a tendency for the limb to move forwards. However, it is prevented from doing so by strong latissimus dorsi and pectoralis muscles,

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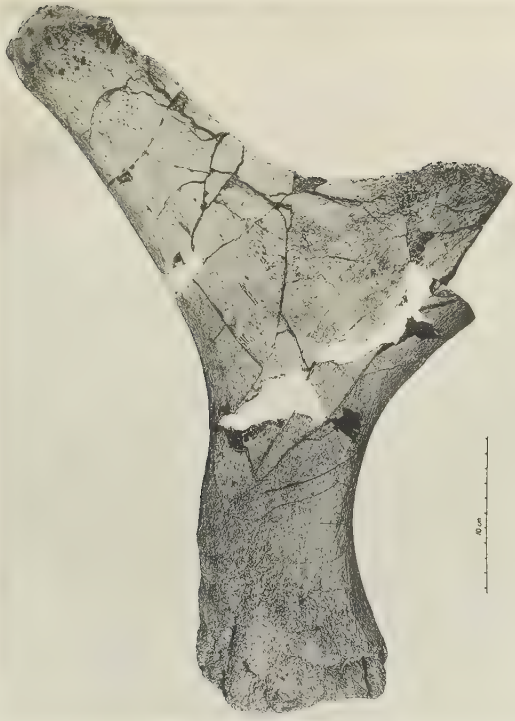
EXPLANATION OF PLATE 37

Figs. 1. 1*a*. *Pliosaurus macromerus*, left scapula, Kimeridge Clay, Stretham, near Ely. 1, dorsal view. 1*a*, ventral view. Sedgk. Mus. J. 35990.

Fig. 2. *Plesiosaurus guilelmi imperatoris* Dames. Reproduction of part of Dames's original figure of the type specimen showing impressions of skin in the forelimb and tail regions.



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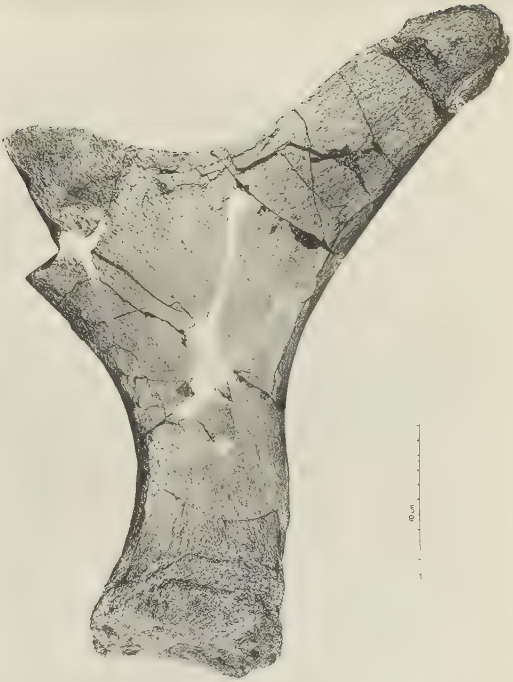

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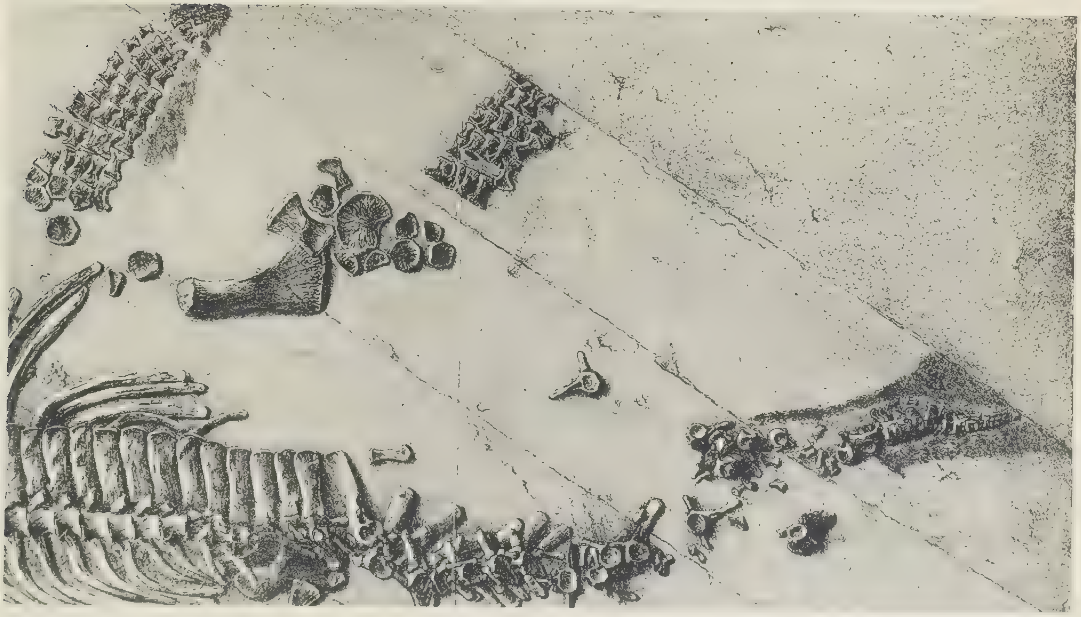

2

TARLO, Jurassic *Pliosaurus* and *Plesiosaurus*

the insertions of which are clearly visible on the humerus. In this way the force tending to move the limb is transmitted to the body, and thus it is not just the forelimb, but the whole body, that moves forward.

At the end of this stroke the limb is adducted backwards by the coracobrachialis muscle, and drawn forward ready for the next swimming stroke by the deltoid, scapulo-humeralis anterior, and subscapularis muscles, the actions of which have already been dealt with in detail.

Also in Dames's figure, the impression of skin in the caudal region seems to indicate that his animal had a ventral fin which followed the line of the muscles, and a dorsal one which flared away from the body. In Pliosaurs too a tail of this sort may have played some part in their locomotion.

The hind limb of the Pliosaur is generally larger than the forelimb and furthermore the ischium is greatly elongated. Thus the area of attachment of the adductor muscles is greatly increased and placed more posteriorly. The large insertion for these muscles in the centre of the ventral surface of the proximal end of the femur indicate that the hind limb is drawn back strongly and pulled in to the body. This produces a powerful propulsive force and together with the hydrofoil-shaped forelimb must have made the Pliosaur a most efficient hunter of the Mesozoic seas.

Acknowledgements. I am greatly indebted to Professor D. M. S. Watson for his valuable guidance, and also to Dr. Pamela L. Robinson, Dr. K. A. Kermack, and Mr. J. Maynard Smith, of University College, London, for the useful discussions I have had with them. I am also pleased to acknowledge the generous assistance I have received from Dr. W. E. Swinton and Mr. B. H. Newman of the British Museum (Nat. Hist.); Dr. C. L. Forbes of the Sedgwick Museum, Cambridge; Mr. J. M. Edmonds of the University Museum, Oxford; and Dr. R. M. C. Eagar of the Manchester Museum. Plate 36, figs. 1, 1*a* was photographed by Mr. M. G. Sawyers; all other photography by Mr. W. Brackenbury. The work embodied in this paper was carried out during the tenure of a D.S.I.R. Research Studentship.

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ONTOGENY OF THE TRILOBITE *PELTURA SCARABAEOIDES* FROM UPPER CAMBRIAN, DENMARK

by H. B. WHITTINGTON

ABSTRACT. Poulsen's original material of the developmental stages of *Peltura scarabaeoides* is redescribed. It includes protaspides of length 0·4 mm. and cranidia or cephala up to a length of 1·6 mm. The protaspid glabella is elliptical in outline, widest at the mid-length, and divided into five rings. In meraspid cephala of length greater than 1 mm. the glabella is widest across the occipital ring and glabellar furrows are lateral. The outline of the anterior cephalic margin changes from forwardly concave to forwardly convex. In a cephalon of length 1 mm. (including occipital spine) the posterior branch of the facial suture crosses the cephalic border immediately outside the base of the fixigenal spine. In a smaller cranidium and the protaspis the exact course cannot be seen, but it may be similar. The fixed cheeks become narrower relative to the occipital ring as size increases, in contrast to their development in other olenids. Fixigenal and median occipital spines are present in a cranidium of length 1·3 mm., but not in larger cranidia. The ontogeny of the cephalon of *P. scarabaeoides* is, among olenids, most like that of *Leptoplastides salteri*.

It was claimed by Poulsen that a considerable migration of the posterior branch of the suture occurred in small cephala of *P. scarabaeoides*. Such a migration cannot be demonstrated, and theoretical deductions based in part on this claim are now open to doubt.

INTRODUCTION

THE view expressed by Poulsen (1927, pp. 330–1) that opisthoparian genera pass through a proparian stage in their ontogeny, was to a large extent based on his investigation (Poulsen 1923, pp. 58–59, 83, fig. 22; 1927, p. 330) of developmental stages of *Peltura scarabaeoides*. In the smallest meraspid head-shield (Pl. 38, fig. 9) the posterior branch of the suture is portrayed by Poulsen as running out from the eye lobe in a curve concave forwards, and crossing the lateral cephalic border at a point in advance of the mid-point of the cephalic length, opposite the second glabellar ring furrow from the anterior. In the next largest cephalon (Pl. 38, fig. 12) the posterior branch is portrayed as running in a curve convex outwards, and crossing the lateral border a short distance in front of the base of the fixigenal spine. In an holaspid cranidium (Pl. 38, fig. 18) the posterior branch crosses the extremity of the posterior cephalic border. Thus the change from a proparian to an opisthoparian sutural condition during ontogeny implied a considerable migration of the point where the posterior branch crosses over the cephalic border and on to the doublure.

The award of a Guggenheim Memorial Fellowship enabled me to visit Copenhagen in May 1957, and Professor Chr. Poulsen afforded me every facility in studying and photographing the original material of *P. scarabaeoides*. I am indebted to Professor Poulsen for his kindness in urging me to publish this redescription. I consider that the smallest post-protaspid developmental stage is a cranidium. The exact course the posterior branch follows cannot be determined. The next largest specimen is a cephalon, and the posterior branch of the suture crosses the border immediately in front of the fixigenal spine, a sutural condition that is usually termed proparian. The considerable change in position of the course followed by the posterior branch of the suture implied in Poulsen's earlier description cannot be demonstrated. It is my opinion that, to

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describe the early developmental stages of *P. scarabaeoides* as proparian may be misleading if by 'proparian' the impression is conveyed that the posterior branch of the suture crosses the lateral cephalic border far in advance of the genal angle. I have discussed elsewhere the ontogeny of other species supposed to show a sutural history like that formerly claimed for *P. scarabaeoides*, marshalled evidence that leads me to believe that they may not go through such a history, and considered the implications of these discoveries (Whittington 1957*a*, *b*). In brief, if the cephala of early meraspides of *P. scarabaeoides* and like trilobites are termed 'proparian', it is only, so far as we know, by virtue of the posterior branch crossing the border immediately in advance of the fixigenal spine. Bearing in mind other morphological characters of these meraspides, it does not seem probable to me that by arrested development they could have given rise to post-Cambrian proparian trilobites.

The terminology used here follows that of earlier papers (e.g. Whittington 1957*a*, fig. 1) and employs the abbreviations sag. (sagittal, in the median line), exs. (exsagittal, parallel to the median line), and tr. (transverse, at right angles to the median line) to define the particular direction under discussion. The new measurements have been made by Professor Poulsen.

Family OLENIDAE Burmeister 1843

Subfamily PELTURINAE Hawle and Corda 1847

Peltura scarabaeoides (Wahlenberg 1821)

Plate 38, figs. 1–18

Material. The originals of Poulsen 1923, pp. 58–59, 83, figs. 22*a–c*, are preserved in four small pieces of black, bituminous limestone (stinkstone or anthraconite) containing abundant parts of trilobite exoskeletons. They are deposited in the Museum of the Mineralogical-Geological Institute, University of Copenhagen, and numbered 1987 (two pieces), 1988 and 1989.

Geological Horizon and Locality. Upper Cambrian Olenid Series, *P. scarabaeoides* zone Vc (Henningsmoen 1957, pp. 237–9, 300) from a well excavation at Lille Duegaard, Aaker parish, island of Bornholm, Denmark. Collected by K. A. Grönwall, Professor Poulsen informs me that the locality is no longer accessible.

Description. Besides the originals of Poulsen (Pl. 38, figs. 1–3, 5, 6), which are 0·42 mm. in length (sag.), there is another protaspis on each of the pieces numbered 1988 and 1989. All four specimens are about the same size, subcircular in outline, strongly convex. Axis divided by furrows into six rings, the anterior furrow shallower than those following. Axis widest across the second ring from the anterior or across the furrow defining this ring posteriorly, tapering progressively anteriorly and posteriorly from greatest width. Frontal lobe and following three rings of about equal length (sag.), strongly convex, next ring posteriorly (occipital) shorter (sag.) but as convex, posterior ring short, much less convex, and situated on steeply-sloping posterior part of shield. Axial furrow well defined, anterior pit shallow. Pleural regions convex, sloping steeply laterally and most steeply posteriorly beside tip of axis. A convex border, defined by a border furrow, bounds the pleural region laterally, and merges postero-laterally into the base of the short, outward and downwardly directed fixigenal spine. Antero-laterally the border becomes wider and less well defined, and is bounded anteriorly by a faint furrow which runs from the anterior pit outward and forward to the margin. In front of this furrow is the tiny anterior border, which narrows and disappears inwards as it approaches the margin of the frontal axial lobe. The posterior margin of the shield, between the bases of the fixigenal spines, is partly concealed and thus ill defined in all the specimens. The outline may be transverse or gently convex posteriorly. In one specimen (Pl. 38, figs. 5, 6) what appears to be a posterior border furrow runs outward (and slightly backward) from opposite the occipital ring furrow to merge distally with the lateral border furrow. Behind this furrow is a faint, low posterior border which runs out opposite the occipital ring and into the base of the fixigenal spine. The protopygidial part of the protaspis is thus short (sag. and exs.) and narrow.

The next largest specimens are of sagittal length, *c.* 0·5 mm. (Pl. 38, figs. 8, 9, the original of fig. 9 measuring 0·54 mm.), there being a third example, showing the short median occipital spine on the smaller piece numbered 1987. Glabella subcylindrical, divided into five rings by furrows which are progressively deeper posteriorly, and only slightly wider across the median than the frontal or occipital ring. Latter ring shorter (sag.) than those in front, which are about equal in length. Deep anterior pit at extremity of deep axial furrow. Anterior cephalic border narrowest in median line, widening progressively distally to give a forwardly concave outline to the anterior margin of the shield. Anterior border furrow runs out from anterior pit. Convex pleural region with lateral and posterior borders well defined by furrows, the borders widening toward the base of the fixigenal spine. This spine is long, directed slightly outward and horizontally (not downwardly as in the protaspis). Palpebral lobe is wider and higher than the adjacent part of the lateral border, clearly defined on the inner side by a palpebral furrow, and continuous at the anterior extremity with a low eye ridge. This latter runs directly inward to reach the axial furrow immediately behind the anterior pit. Surface of pleural region coarsely granulate.

The next largest specimen is of a cephalon with the free cheeks only slightly displaced

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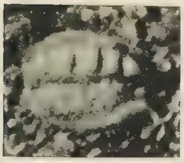
EXPLANATION OF PLATE 38

Fig. 1–18. *Peltura scarabaeoides* (Wahlenberg), Upper Cambrian Olenid Series, Bornholm, Denmark. Catalogue numbers of the Museum of the Mineralogical-Geological Institute, University of Copenhagen. 1–3, protaspis, latero-dorsal, dorsal, postero-dorsal views, no. 1987, original of Poulsen 1923, fig. 22*a*, left, ×40. 4, protaspis, partial reconstruction in dorsal view, *c.* ×54. ab = anterior border, ap = anterior pit, fx = fixigenal spine, lb = lateral border of pleural region, or = occipital ring, pb = posterior border of cephalon, pl = palpebral lobe. 5, 6, protaspis, postero-dorsal and dorsal views, no. 1987, original of Poulsen 1923, fig. 22*a*, right, ×40. 7, protaspis, reconstruction in latero-dorsal view, *c.* ×54. *a* = supposed point where anterior branch of suture crosses margin of anterior border, *b* = supposed point where posterior branch of suture crosses margin of lateral border. Other letters as in fig. 4. Dashed line indicates position of margin of hypothetical free cheek. 8, incomplete cranidium, dorsal view, no. 1987, ×30. 9, cranidium, dorsal view, no. 1988, original of Poulsen 1923, fig. 22*b*, left, ×30. 10, cranidium, dorsal view, based on original of fig. 9, *c.* ×40. abs = anterior branch of suture, er = eye ridge, pbs = supposed course of posterior branch of suture, sr = sutural ridge. Other letters as in fig. 4. Dashed line indicates supposed position of margin of free cheek. 11, 12, cephalon, latero-dorsal and dorsal views, no. 1988, original of Poulsen 1923, fig. 22*b*, right, ×30. 13, cephalon, dorsal view, based on original of fig. 12, *c.* ×28. Letters as in figs. 4, 10. 14, external mould of incomplete cranidium, oblique view, no. 1989, ×15. 15, 18, cranidium, anterior and dorsal views, no. 1989, original of Poulsen 1923, fig. 22*c*, ×15. 16, incomplete free cheek, oblique view, no. 1989, ×15. 17, incomplete free cheek, oblique view, no. 1988, ×15.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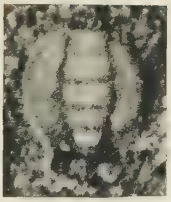
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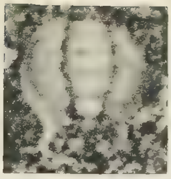
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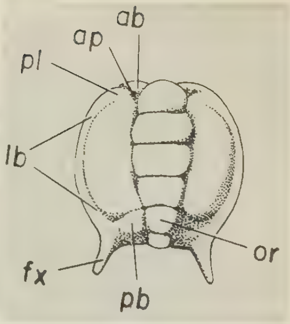

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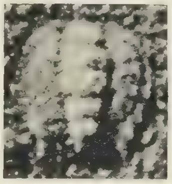
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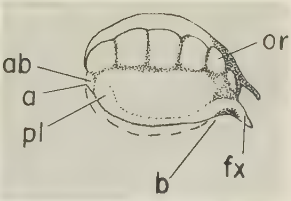

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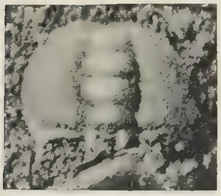
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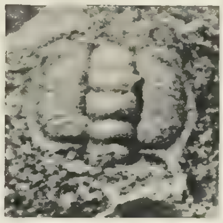
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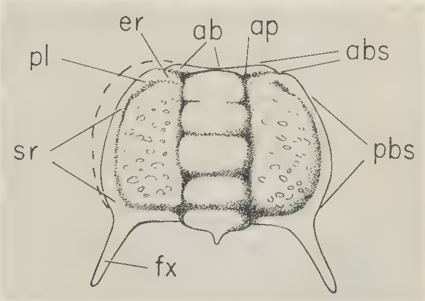

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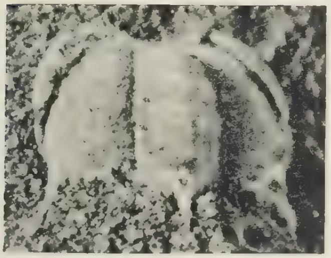
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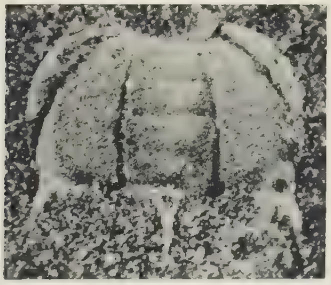
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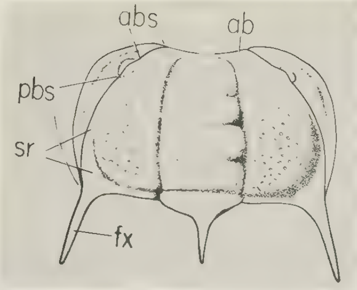

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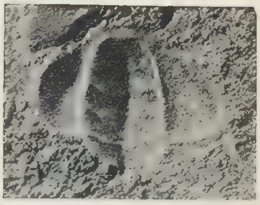
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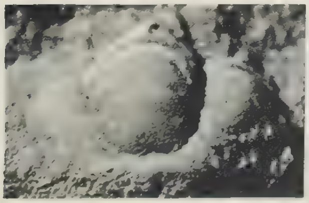
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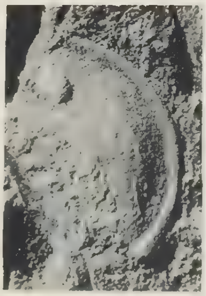
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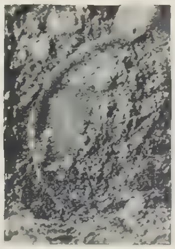
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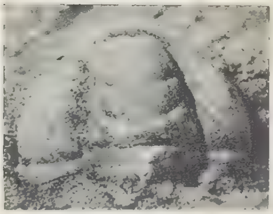
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WHITTINGTON *Peltura scarabaeoides*

(Pl. 38, figs. 11, 12). Length (sag.), including median occipital spine, 1·02 mm. Glabella divided by shallow furrows into five rings, occipital furrow deeper than those in front and occipital ring shorter (sag.) than the rings anterior to it. Glabella widest across median ring, tapering markedly to frontal lobe and only slightly to occipital ring. Anterior pit faint. Anterior border narrowest at mid-line, widening and curving forward distally to give concave anterior marginal outline to cephalon. Long fixigenal and median occipital spines. A low broad ridge runs forward from the base of the fixigenal spine, following the course of the posterior branch of the suture, and dies out at about the mid-length of the fixed cheek. Palpebral lobe and eye ridge low and ill defined. Free cheek widest (tr.) opposite eye lobe, low border defined by shallow furrow. Course of anterior and posterior branch of suture clearly shown by displacement of free cheeks, and posterior branch curves back to cross the margin of the pleural region at the outer edge of the base of the fixigenal spine.

Larger specimens include cranidia of length 1·33 mm. (Pl. 38, fig. 14) and 1·56 mm. (Pl. 38, figs. 15, 18) and incomplete free cheeks (Pl. 38, figs. 16, 17). The smaller of these cranidia has the glabella crossed only by the occipital furrow (across which it is widest), first and second lateral glabellar furrows extending diagonally inward about one-third the width, and faint third furrows. The anterior marginal outline of the cranidium is convex forward, there is a short median occipital spine and a longer fixigenal. The larger cranidium is of the same general form, the third glabellar furrow extremely faint, palpebral lobe opposite this furrow, and eye ridge faint. Median occipital tubercle and short median spine immediately behind it. Fixigenal spine absent.

The largest cranidium and free cheek in the Danish material is one-third or less the size of specimens of the typical sub-species illustrated by Henningsmoen (1957, pl. 25, fig. 13; pl. 26, fig. 1). Comparisons with these figures suggest that, as size increases, the glabella assumes a sub-square rather than sub-conical outline, and becomes relatively wider. The free cheek changes in outline so that the postero-lateral curvature of the margin is greater, and the maximum width farther back.

Discussion. My interpretation of the protaspis and two succeeding stages is shown in Pl. 38, figs. 4, 7, 10, 13. Facial sutures can first be observed unequivocally in the small cephalon (Pl. 38, figs. 11, 12). A low ridge runs forward from the base of the fixigenal spine along the border of the cranidium and dies out at about half the length. At least the anterior part of this ridge may be a structure distinct from the cephalic border (best preserved on the right free cheek), and is so shown in Pl. 38, fig. 13. The ridge is termed the sutural ridge because it runs beside the suture. In larger specimens the sutural ridge is extremely faint (Pl. 38, fig. 14) or cannot be distinguished (Pl. 38, fig. 18). In the next smallest specimens (Pl. 38, figs. 8, 9) the sutural ridge is well defined and extends forward to form a continuous structure with the eye lobe (and hence at least the anterior part of the sutural ridge may be a structure distinct from the lateral cephalic border, which in later developmental stages may be seen to run outside the eye lobe). It appears to me that this specimen is a cranidium, bounded laterally by the two branches of the suture. How far back the posterior branch extended before crossing over the margin of the cephalon and on to the doublure is a matter that cannot be decided from the available material. I have suggested a course analogous to that in the next largest specimen, and the possible outline of the free cheek by a dashed line.

In the protaspis (Pl. 38, figs. 4, 7) I suggest that the slightly wider, antero-lateral part of the border is the palpebral lobe, and that the remainder of the lateral border represents the sutural ridge of larger specimens. If sutures were developed, as they are in other small protaspides (Whittington 1957*a*), they may have followed a course along the outermost parts of the pleural regions. The shape of the distal part of the anterior border suggests that there may have been a suture which ran from the point *a* in Pl. 38, fig. 7, across the anterior border, bounded the palpebral lobe, and extended an unknown distance back along the lateral pleural border (= sutural ridge of larger specimens). In lateral view (Pl. 38, fig. 1) this border is wide for a short distance in front of the fixigenal spine, then narrows rather abruptly. I suggest that this change in width is determined by the suture extending back on the dorsal side to the point *b* in Pl. 38, fig. 7, before it crosses on to the doublure. I have also indicated an outline of the hypothetical free cheek consistent with these views.

Authors are agreed that the sutural condition of holaspid *Peltura* should be termed 'opisthoparian'. In larger specimens than those illustrated here (e.g. Henningsmoen 1957, pl. 2, fig. 1) the outline of the postero-lateral part of the free cheek is strongly angular, giving a decisively 'opisthoparian' appearance to the cephalon. It is also prevailing practice to term an olenid cephalon 'proparian' if a fixigenal spine is present and the suture crosses the margin just outside the base of this spine (e.g. *Saltaspis* in Henningsmoen 1957, p. 244, pl. 2, fig. 11; Harrington and Leanza 1957, p. 93, fig. 31). Thus the original of the present Pl. 38, fig. 12 may likewise be termed 'proparian', and one may continue to say that *P. scarabaeoides* exhibits the proparian condition in early developmental stages. However, the point where the posterior branch of the suture crosses the cephalic border in the original of Pl. 38, fig. 12 is similarly situated to that in small cranidia of *Flexicalymene* (Whittington 1941, pl. 72, fig. 4)—a disputed 'proparian'—but is far posterior to that in such 'typical' proparia as phacopids or cheirurids (Whittington 1957*a*, figs. 16, 18). It appears to me that a mistaken impression may thus arise from characterizing the early stages of *P. scarabaeoides* as 'proparian'. The course followed by the posterior branch in the protaspis and earliest known meraspis remains open to conjecture, but I have surmised (Pl. 38, figs. 7, 10) that it may have been much the same as in the small cephalon (Pl. 38, fig. 12).

Among olenids the protaspid and meraspid development of *Olenus gibbosus* is known (Strand 1927; Størmer 1942), and the development from meraspid degree 1 onwards of *Leptoplastides salteri* (Raw 1925) and *Triarthrus eatoni* (Whittington 1957*a*, *b*). The protaspis of *O. gibbosus*, of the same size as that here described of *P. scarabaeoides*, has the same general form, but the outline of the glabella is strikingly different, being widest anteriorly and tapering back to the occipital ring. The pleural border (= sutural ridge) is present only postero-laterally in *O. gibbosus*, and the spines on the posterior border, possibly fixigenal, are small. Meraspid cranidia of about 0·5 mm. length of *O. gibbosus* differ principally from those of *P. scarabaeoides* in having the frontal glabellar lobe the widest, and this lobe exhibits both a short lateral furrow at the mid-length and a short median anterior furrow. The anterior cranidial margin in *O. gibbosus* is straight, and the sutural ridge and a tiny fixigenal spine are present. Cranidia of *O. gibbosus* of about 1·0 mm. length are distinguished by the presence of the pre-glabellar field, more prominent palpebral lobe and eye ridge, and absence of fixigenal spine.

Cephala of *L. salteri* of meraspid degrees 3 and 5 are of about the same size as the originals of Pl. 38, figs. 9 and 13 respectively. Those of *L. salteri* have the glabella similar to that of *P. scarabaeoides*, but are distinguished by the stronger eye ridges, presence of short preglabellar field, anterior cephalic and librigenal spines, and the lack of sutural ridges.

The degree 1 cranidium of *T. eatoni* is 0·6 mm. in length, and those of degrees 3–5 range from 0·9 to 1·2 mm. in length. They are distinguished from cranidia of comparable size of *P. scarabaeoides* by the forwardly expanding glabella, differing glabellar lobation, lack of anterior border furrow, forwardly convex outline of the anterior cranidial margin, and absence of fixigenal spine and sutural ridge.

The ontogeny of the cephalon of *L. salteri* is most like that of *P. scarabaeoides*, especially in the axial region, and these two genera are placed in the same subfamily of Olenidae by Henningsmoen (1957, p. 18). The growth of the axial cephalic region is different in *O. gibbosus* and *T. eatoni*, and evidently in olenids the amount of growth displayed by the frontal area may vary greatly. The considerable change in the cephalic outline during ontogeny of *P. scarabaeoides* is notable—from a bow-shaped anterior and antero-lateral margin to a curve convex forward. The early cephalic outline is one particularly characteristic of holaspid *Ctenopyge* cephala. Henningsmoen (1957, p. 90) remarks that in certain species of olenids 'large cranidia have relatively wider fixed cheeks than smaller cranidia'. In *P. scarabaeoides* the opposite is the case. The proportion between width of occipital ring and width of fixed cheek at posterior border is 0·96 in the small cranidia (Pl. 38, fig. 9) and 2·9 in a large holaspid figured by Henningsmoen (1957, pl. 26, fig. 1), and 2·5 in an holaspid of *P. scarabaeoides westergårdi* (Henningsmoen 1957, pl. 25, fig. 10).

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ADDENDUM

Since the above paper was submitted to the Editor, an account of the ontogeny of the Lower Cambrian ptychoparioid trilobite *Crassifimbra walcotti* has been published by Dr. A. R. Palmer (*J. Paleont.* **32,** 154–70). The series is more complete than that of *Peltura scarabaeoides* and beautifully preserved. The smallest protaspis of *C. walcotti* is of the same size as that of *P. scarabaeoides*, and has a similar lateral border. The dorsal part of the free cheek is a short (exs.) and extremely narrow (tr.) portion of this lateral border, the posterior branch of the suture crossing the margin at about the mid-length, the condition thus being decisively proparian. The smallest meraspid cephala of *C. walcotti* are the same size as the smallest cranidium of *P. scarabaeoides* (Pl. 38, figs. 8–10), but lack the sutural ridges of the latter. The posterior branch of the suture in *C. walcotti* cuts the margin at the postero-lateral corner of the cephalon and the free cheek is narrow—as postulated in *P. scarabaeoides*. Since neither fixigenal nor librigenal spines are present in *C. walcotti*, Palmer terms the sutural condition gonatoparian. In the middle meraspid and later developmental stages a librigenal spine develops, and the sutural condition is then opisthoparian.

THE GENUS *ARCHAIAS* (FORAMINIFERA) AND ITS STRATIGRAPHICAL DISTRIBUTION

by A. H. SMOUT AND F. E. EAMES

ABSTRACT. The genus *Archaias* Montfort 1808 was emended by Henson 1950. It includes those species of the Family Peneroplidae which have chambers that contain interseptal pillars but no subepidermal partitions. All species are reviewed and described as far as possible. Additional illustrations are given for Middle East species. The stratigraphical occurrences are also considered.

The genera *Helenis* Montfort 1808, *Ilotes* Montfort 1808, *Orbiculina* Lamarck 1816 (as by previous authors), and *Puteolina* Hofker 1952*a* (*min. pars*) are placed in the synonymy of *Archaias*. *Cyclorbiculina* Silvestri 1937 is not, contrary to usage in leading textbooks.

Species of *Archaias*

(*a*) Valid species:
- *Nautilus angulatus* Fichtel and Moll 1798.
- *Archaias asmaricus* sp. nov.
- *Nummulites floridanus* Conrad 1846.
- *Archaias hensoni* sp. nov.
- *Archaias kirkukensis* Henson 1950.
- *Archaias operculiniformis* Henson 1950.

(*b*) Probable valid species (description inadequate):
Archaias columbiensis Applin and Jordan 1945

(*c*) Species removed from *Archaias*:
Orbiculina adunca var. *flabelliformis* Lister 1903 = *Cyclorbiculina compressa.*
Orbiculina compressa d'Orbigny 1839 = *Cyclorbiculina compressa.*
Orbitolites malabarica Carter 1853 = *Taberina malabarica.*
Orbiculina mamillata Carter 1857 = *Orbitolinopsis sp.* (Provisionally used for *Orbitolina* auctt. because the type species *O. gigantea* d'Orbigny 1857 is a coral.)
Orbiculina rotella d'Orbigny 1846 = *Borelis sp.*
Archaias vandervlerki de Neve 1947 = *Taberina malabarica.*

(*d*) Invalid names (all synonyms of *A. angulatus*):
- *Nautilus aduncus* Fichtel and Moll 1798.
- *Orbiculina numismalis* Lamarck 1822.
- *Orbiculina nummata* Lamarck 1816.
- *Nautilus orbiculus* Fichtel and Moll 1798, *non* Forskål 1775.
- *Ilotes rotalitatus* Montfort 1808.
- *Helenis spatosus* Montfort 1808.
- *Archaias spirans* Montfort 1808.
- *Orbiculina uncinata* Lamarck 1822.

INTRODUCTION

DURING the course of investigations into the Asmari Limestone of Iran and the Main Limestone of Iraq it was found that recognition of *Archaias spp.* gave considerable difficulty. It is now possible to support with additional figures and more complete descriptions the species published by Henson (1950). Two other species mentioned but not formally named by Henson can now be recognized. In the Middle East it is rare to find separate specimens of *Archaias spp.* and even rarer to find ones with visible external structure. The only practical utility of these species is in random thin sections. The difficulties of diagnosis are accentuated by damage to the specimens before and during fossilization, and as found the test is often not a distinct structure but merely an alteration product in hard limestone. The variability of species of the Peneroplidae is notorious and one must always expect a proportion of aberrant specimens. Considerable familiarity with Recent Peneroplidae is highly advisable before attempting determination of such fossil material. Apparently good sections are sometimes difficult to interpret; for

[Palaeontology, Vol. 1, Part 3, pp. 207–25. pls. 39–41, 42 (pars)]

instance, a specimen with a single equatorial row of pillars would give an appearance of having several rows in a section only slightly oblique to the equatorial plane and would show every chamber crowded with pillars in true equatorial section. An axial section usually appears to have more whorls than would be shown by the same test in equatorial sections. This is because the alar prolongations of the chambers are vorticiform and their curvature adds from a quarter to two apparent whorls to the actual spire, particularly when there is a large reniform stage. Cyclical chambers are strictly evolute, but where spiral chambers are strongly curved or there are reniform chambers it may be possible to prepare sections that cut many chambers on both sides of the centre while avoiding alar prolongations, except in the inner whorls. This pseudevolute condition cannot always be distinguished from the true evolute condition. Sections always tend to show a smaller diameter for the nucleoconch than the true one because they are usually slightly out of the exact centre line. The preponderant type of section is related to the shape of the test; some species are seen in random section as more or less axial sections, with rare exceptions, while other species show a high proportion of specimens that look highly oblique or even approximately equatorial. This is caused by the variation in angle from the axial or equatorial section, which is tolerable before the appearance is noticeably changed. In general it is unwise to determine a single specimen; a suite of specimens usually enables one to determine the dominant species but leaves a possibility that related species are present in small numbers.

The distribution of species in the Middle East has definite stratigraphical value. *A. operculiniformis* occurs in the earlier Oligocene (Lattorfian? and Rupelian) and one occurrence in the higher part of the Oligocene (Chattian) has been noticed by us. *A. kirkukensis*, *A. asmaricus*, and *A. hensoni* occur at higher horizons, and overlap with *A. operculiniformis* has not been recognized; their age is given as U. Oligocene and perhaps Lower Miocene by Henson (1950), and Van Bellen (1956) recorded *A. kirkukensis* as ? Middle or Upper Oligocene.

In Gach Saran Wells 6 and 11 of Iran, *A. kirkukensis* is common in the lower part of the Middle Asmari Limestone, while *A. asmaricus* and *A. hensoni* are common in the higher part. Specimens doubtfully assigned to all three species were found throughout. Occurrences in Iraq are mostly of one species in any one section. In the Bajawan Limestone of Kirkuk Well 21, *A. kirkukensis* occurs in abundance, and *A. asmaricus* alone occurs at a slightly higher level (*c.* 20 ft.) in the same formation. Distinction between the Anah and Bajawan formations given here is not always based on conclusive evidence.

The European Stage names used here are intended only as an approximate guide to age. They are used in preference to subdivisions of the Oligocene, which are subject to differences of convention and are even less susceptible to precise definition. We do, however, follow the trend of current opinion in regarding the Aquitanian as Lower Miocene; in Iran the Middle Asmari Limestone (here regarded as Aquitanian in age) immediately underlies beds of Burdigalian age, often in normal succession. Its fauna, which includes *Meandropsina anahensis* Henson 1950 and *Austrotrillina howchini* (Schlumberger) 1893 *sensu stricto*, is definitely more closely related to Burdigalian than to Oligocene faunas. It has in common with the Oligocene of the Middle East the species *Praerhapydionina delicata* Henson 1950, *Peneroplis evolutus* Henson 1950, *P. thomasi* Henson 1950, and *Borelis pygmaea* Hanzawa 1930, but these species are known also from Miocene beds in other areas.

The evolution of species of *Archaias* is not known with certainty. *A. columbiensis* and *A. operculiniformis* may have belonged to the same lineage but were more probably evolved independently from lenticular species of *Peneroplis* such as *P. dusenburyi*. *A. kirkukensis* may have evolved from *P. evolutus*, which has a similar spire; Henson (1950) suggested its derivation from *P. thomasi*, but we think this must have been a *lapsus calami*. *A. asmaricus* so closely resembles *P. thomasi*, which has a longer, overlapping range, that there can be little doubt that it was evolved from that species. *A. hensoni* may be related to *A. kirkukensis*. *A. floridanus* was most probably independently evolved in the West Indies seas and it is possible that *A. angulatus* is descended from *A. floridanus*. There is no reason to assume a close phyletic relationship to the peneroplid species with subepidermal partitions, although there has been extensive taxonomic confusion between species of the two groups.

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DESCRIPTIVE PALAEONTOLOGY

ARCHAIAS Montfort 1808, emended Henson 1950

Helenis Montfort 1808, pp. 194–5 (type species *H. spatosus* Montfort 1808).
Ilotes Montfort 1808, pp. 198–9 (type species *I. rotalitatus* Montfort 1808).
Orbiculina Lamarck 1816, p. 14 (type species *Nautilus aduncus* Fichtel and Moll 1798).
Puteolina Hofker 1952 (*min. pars*), p. 450 (type species *Peneroplis proteus* d'Orbigny 1839, p. 60, pl. 7, figs. 7–11).

Type species Nautilus angulatus Fichtel and Moll 1798 = *Archaias spirans* Montfort 1808.

Diagnosis. The test is composed of porcellaneous shell material, very finely pitted, but perforate only in the very early stages. The chamber walls are distinct and there is no thickening. Interseptal pillars are present in most chambers but there are never subepidermal partitions or secondary septa. The earliest chambers may be empty of pillars and the later ones may be brood chambers with enlarged lumina and reduced pillars. Intercalary whorls have not been recorded in this genus; the spire is always simple and planispiral, typically beginning with a closely-coiled stage, passing through a laxispiral stage and ending with a terminal flare. Some species develop flabelliform or cyclical chambers. The spiral chambers are equitant and mostly fully involute, but in the last whorl the alar prolongations may retreat from the poles. The flare of the spire often results in a central involute boss and a large pseudevolute flange, while cyclical chambers are always evolute. The chambers are usually curved and the alar prolongations verticiform. This, combined with the radial direction of the margin when the spire becomes aduncate, causes the apparent margin of the adult test to be mostly truncate and occupied by the apertural face, whereas the true margin is rounded. The apertures of the early chambers are basal slits but in most chambers the apertures consist of rows of pores. All known species are dimorphic or trimorphic. The megalosphere is spherical or subspherical and is followed by a distally swollen neck-chamber which in some species is coiled at an angle to the equatorial plane.

Remarks. Following Henson (1950), we define *Archaias* as containing those species of the Peneroplidae that have interseptal pillars in the chambers but no subepidermal partitions or secondary septa.

The original description of the species mentioned subdivided chambers, and it was assumed that these were a normal feature of the genus until Henson demonstrated that the type species had pillars but no subepidermal or other partitions in the chambers. Hofker (1952) confirmed this. It will be found from the synonymy of *A. angulatus* (given below) that this is indeed the true species and, from the redescription, that it is a very distinct species which does not intergrade with any that have subepidermal partitions, in spite of published statements to that effect, e.g. d'Orbigny (1839), Brady (1884), Lister (1903). No known case exists in which such intergradation is suspected and therefore Henson's revision of the genus is maintained, although it differs drastically from all earlier ones.

From the synonymy of *Archaias angulatus* it follows that the genera *Helenis* Montfort 1808, *Ilotes* Montfort 1808, and *Orbiculina* Lamarck 1816 are junior synonyms of *Archaias*.

Cyclorbiculina Silvestri 1937 (type species *Orbiculina compressa* d'Orbigny 1839) has been placed in the synonymy of *Archaias* in many textbooks. This was justified by the usage current before 1950, but becomes impossible after Henson's generic revision. *O. compressa* commonly occurs with *A. angulatus* and has been extensively confused with it, being one of the species with subepidermal partitions that have given rise to misconceptions about the characters of the genus *Archaias*.

Puteolina Hofker 1952 (type species *Peneroplis proteus* d'Orbigny 1839) includes *Archaias angulatus* in the original list of species and Hofker treats *Archaias* as a subgenus of *Puteolina*. *Puteolina* is therefore in part a synonym of *Archaias*. In addition to the nominal defect, we do not consider the relationships of the species involved to be well expressed by Hofker's taxonomic treatment.

Occurrence. Middle Eocene to Recent, tropical to subtropical seas.

Archaias angulatus Fichtel and Moll 1798

Plate 39, figs. 1–5

Nautilus orbiculus Fichtel and Moll 1798, p. 112, pl. 21, figs. *a–d*, *non* Forskål 1775, p. 125.
N. angulatus Fichtel and Moll 1798, p. 113, pl. 22, figs. *a–e*.
N. aduncus Fichtel and Moll 1798, p. 115, pl. 23, figs. *a–e*.
Archaias spirans Montfort 1808, p. 190 (pl.), p. 192.
Helenis spatosus Montfort 1808, p. 194 (pl.), pp. 195–6.
Ilotes rotalitatus Montfort 1808, p. 198 (pl.), 199–200.
Orbiculina adunca (Fichtel and Moll); Lamarck 1816, p. 14.
O. nummata Lamarck 1816, p. 14, pl. 468, figs. 1*a–d*.
O. numismalis Lamarck 1822, p. 609, pl. 21, figs. *a–d*.
O. uncinata Lamarck 1822, p. 610, pl. 23, figs. *a–e*.
O. adunca (Fichtel and Moll); d'Orbigny, *in* de la Sagre 1839, pp. 81–83, pl. 8, figs. 8, 9, 14; *non* 10–13, 15–16.

O. adunca (Fichtel and Moll); Carpenter 1862, pp. 93–99, pl. 8, figs. 7–12, *non* 1–6.
O. adunca (Fichtel and Moll); Brady 1884, pp. 62, 132, 208–9, pl. 14, figs. 1, 2, 5, 6, 10–13, *non* 3, 4, 7–9.
O. adunca (Fichtel and Moll); Flint 1899, p. 304, pl. 50, fig. 1 part.
O. adunca (Fichtel and Moll); Lister 1903, pp. 96–97 part.
O. adunca (Fichtel and Moll); Cushman 1918, pp. 84–85, pl. 33, fig. 3.
Archaias angulatus (Fichtel and Moll); Cushman 1930, p. 46, pl. 16, figs. 1–3, pl. 17, figs. 3–5.
Puteolina (*Archaias*) *angulata* (Fichtel and Moll); Hofker 1952*a*, pp. 461–3, figs. 49–51, *non* 50*b*.

Description. The test is complanate with a median swelling and a large pseudevolute flange. The spire has about $4\frac{1}{2}$ whorls in the microspheric test, the first being closely coiled but the later ones becoming lax, the last forming a flare so that the direction becomes radial and an aduncate termination is formed. All chambers are equitant and the septa are strongly curved. Most chambers are involute to the poles and the alar prolongations follow the spiral set by the septa. The alar prolongations subtend less than a quadrant each. The terminal quadrant of the test has the alar prolongations progressively shortened so that the last ones just overlap on to the disk. An adult test shows slightly depressed septal sutures, and often only the radially directed terminal part of the spire is visible externally. It is very easy to misunderstand the structure and to mistake septa for spire. The only ornament is of very fine, closely crowded pits. The margin of the test is truncate where occupied by the apertural face, rounded where truly marginal. The apertures of the earliest chambers are basal slits, but later chambers have one or two rows of apertural pores along the elongated apertural face. The last four chambers are brood chambers with a greater distance between septa than normal, and with sparse pillars or none at all. Nearly all chambers have interseptal pillars, which have slight ridges running from them towards the edge of the septa. The microspheric form has more than one whorl of juvenile chambers without pillars. The megalospheric test is closely similar to the microspheric one, grows to about two-thirds the size, and has about $3\frac{1}{2}$ whorls; it also has an aduncate termination to the spire. This species is trimorphic and the A1 generation has up to three juvenile chambers without pillars, whereas the A2 generation has all chambers after the neck chamber pillared. The proloculus is always subspherical and the neck chamber is widest proximally; Hofker shows it subtending about 270° but specimens have been seen with it subtending only 90°, while no specimens of the longer type have been seen by us. Possibly this is a character liable to local variation. Brood chambers have not been seen in the megalospheric generation.

Dimensions

Distance between the centres of septa: 0·05 to 0·07 mm.
Average diameter of pits: 0·004 mm.
Pit spacing between centres about 0·01 mm.

Microspheric test:	Whorl no.	1	2	3	4	5
	Septa	?	13	15	23	35

Maximum diameter of test at least 6·0 mm.
About 4 brood chambers, about 0·14 mm. high.
Proloculus diameter 0·01 mm. *fide* Hofker 1952*a*.

Megalospheric test:	Whorl no.	1	2	3	4
	Septa of A2	1	12	18	12

Diameter of A2 megalosphere up to 0·16 mm. *fide* Hofker 1952*a*.
Diameter of whole nucleoconch of A2 form 0·23 to 0·15 mm.
Diameter of whole nucleoconch of A1 form about 0·045 mm.

Remarks. Nautilus orbiculus Fichtel and Moll 1798 is a junior homonym of *Nautilus orbiculus* Forskål 1775, which is a well-known species that occurs off the coasts of Arabia and East Africa, in the Mediterranean Sea, and in other areas; it is now commonly known as *Sorites orbiculus* (Forskål). In the same paper Fichtel and Moll described and figured *Nautilus angulatus* and *N. aduncus*. Montfort (1808), who frequently renamed species for no obvious reason, proposed the names *Archaias spirans*, *Helenis spatosus*, and *Ilotes rotalitatus* respectively for Fichtel and Moll's three species. *Orbiculina* Lamarck 1816 was presumably proposed in ignorance of the availability of Montfort's three genera.

D'Orbigny 1839 stated that *N. orbiculus*, *N. angulatus*, and *N. aduncus* are growth stages of one species, for which he adopted the name *Orbiculina adunca*. It is noteworthy that he was working on material from the West Indies. He described another species from the West Indies as *Orbiculina compressa* but, to judge from his plates, he did not correctly separate the species from '*O. adunca*'. *O. compressa* differs from *A. angulatus* in having subepidermal partitions, and the terminal flare of the spire occurs at a relatively small size, succeeding chambers being either reniform, flabelliform, or cyclical. Brady (1884), Flint (1899), and Lister (1903) all confuse the two species, referring both to *O. adunca*. Cushman (1917) recorded *O. adunca* from the North Pacific but the determination cannot now be confirmed. Cushman (1918) recorded *O. adunca* from the Pleistocene of the Panama Canal Zone, probably correctly.

Cushman 1930, identified *Archaias angulatus*, gave a correct synonymy, and clearly distinguished the species from *O. compressa*. He recorded Recent specimens from waters off Bermuda, Cuba, Porto Rico, Bahamas, Jamaica, and Florida. He also records fossil occurrences in the West Indies, Panama, and Florida, but these are suspect of confusion with *A. floridanus*, particularly those from the Miocene. The specimen figured by Hofker 1952*a*, p. 461, fig. 50*b* is probably *A. floridanus*, not *A. angulatus*.

There has previously been no complete and accurate description of *Archaias angulatus*, although a selective combination of details from Cushman (1930), Henson (1950), and Hofker (1952*a*) would constitute one. Cushman (1930) gave adequate illustrations to make the recognition of *A. angulatus* possible, and the synonymy indicates that, if the species are correctly identified, his choice of name is correct. There are two major difficulties to be overcome. First, Fichtel and Moll (1798) state that *N. orbiculus* was found in the Mediterranean while *N. angulatus* and *N. aduncus* occurred in the Arabian

EXPLANATION OF PLATE 39

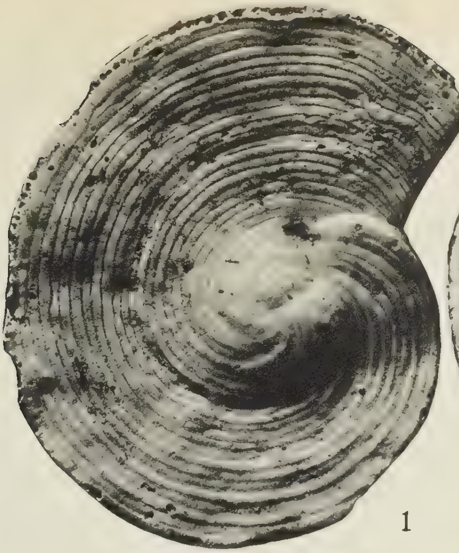
All figures magnified × 20 except Fig. 4 which is × 13.

Figs. 1–5. *Archaias angulatus* (Fichtel and Moll) 1798. Off Barbados; Recent. 1, Exterior of megalospheric test (P. 43706). 2, Equatorial section, megalospheric test (P. 43660). 3, Axial section, megalospheric test (P. 43661). 4, Equatorial section, micropheric test, × 13 (P. 43662). 5, Tangential section parallel to the equatorial plane, megalospheric test (P. 43663).

Figs. 6–9. *Archaias operculiniformis* Henson 1950. 6, 7, Oblique sections, showing the terminal flare and brood-chambers, megalospheric tests; Kirkuk Well 14, Iraq; Shurau Limestone (Oligocene); (6—P. 43707; 7—P. 43664). 8, 9, Axial and equatorial sections, microspheric tests; syntypes (after Henson 1950); Kuh-i-Khamir, Iran; lower part of Khamir Limestone (Oligocene); 8—P. 39712; 9—P. 39711).

Figs. 10, 11. *Archaias sp.* The determination of these apparently good specimens is difficult; (10 after Henson 1950); near Anah, west Iraq; horizon unknown (10—P. 39653; 11—P. 43708).

Numbers in brackets are the registration numbers of the specimens/slides in the British Museum (Natural History).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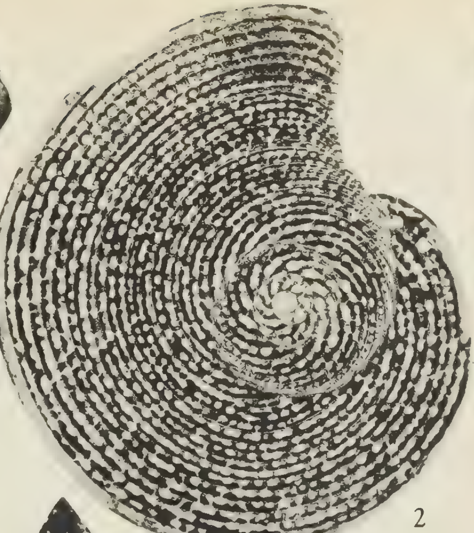
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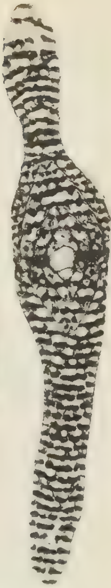
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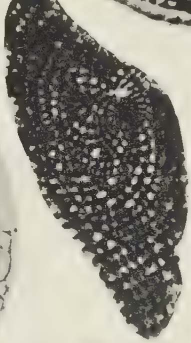
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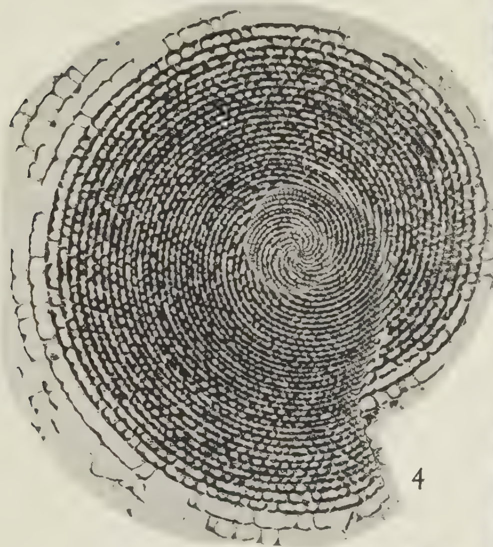
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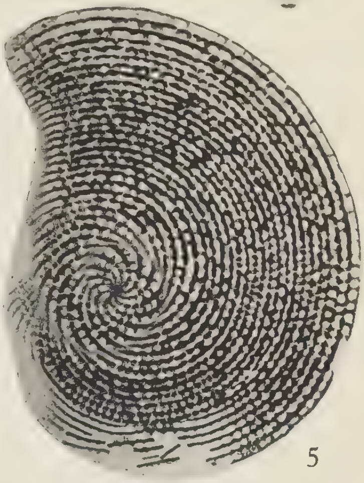
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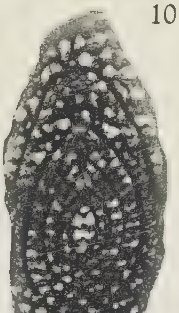
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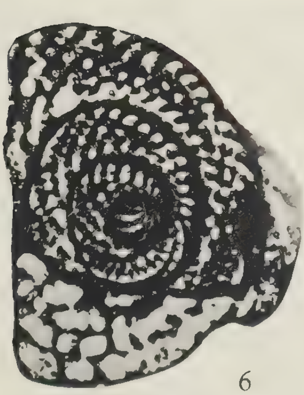
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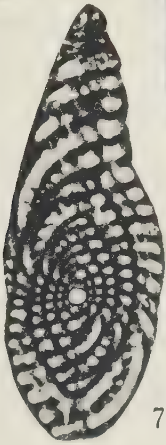
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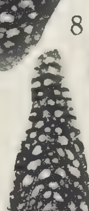
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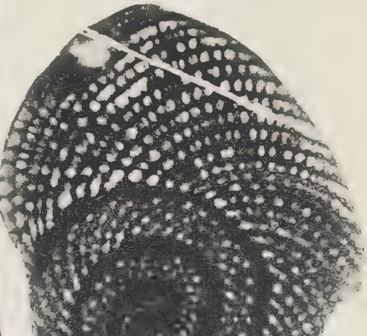
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SMOUT AND EAMES, *Archaias*

Sea. The Caribbean species here called *A. angulatus* is found only in that province and certainly does not occur either in the Mediterranean or in the Arabian Sea. Cushman (1930, p. 47) remarked 'There is much question as to its occurrence in the Mediterranean, and it may be that the authors had West Indian material from some source'. This indeed must have been the case. Both of us, and Dr. Henson, have had many opportunities to find or acquire specimens from Arabia, Africa, India, and the Mediterranean had any existed. It must then be questioned: were Fichtel and Moll's specimens, which are now lost, the same species as that now known as *Archaias angulatus*? Fortunately we have d'Orbigny's identification, although this included specimens of other species which do not seem to have contributed to Fichtel and Moll's plates but possibly did to their descriptions. We have made a careful comparison of these plates with all living species of Peneroplidae and are satisfied that *Nautilus orbiculus*, *N. angulatus*, and *N. aduncus* all represent the same species and that its identification is correct. One must look at these early drawings with the realization that the artist was attempting to illustrate an appearance not a theoretical structure, and that the figures are not to any one scale. The original descriptions and those of many other authors refer to subdivided chambers in this species, but Henson (1950) pointed out that only pillars and not subepidermal partitions were to be found in the chambers; this was confirmed by Hofker (1952*a*). Since the numerous pillars in the chambers can look very like partitions and it requires careful scrutiny to distinguish the two, the errors of description are not surprising. When it is also remembered that *Cyclorbiculina compressa* is usually present in the samples and has subepidermal partitions in the chambers, the error is all too easy to make. All records of cyclical chambers in *A. angulatus* also seem to be based on misidentification of *C. compressa*. Correctly identified flabelliform specimens are rare and most if not all records are based on specimens of *C. compressa* or *Peneroplis proteus*. We have not observed specimens with brood chambers completely devoid of pillars, as stated by Henson (1950). The pillars are usually much reduced, however, and total elimination in some specimens would not be unexpected.

Records of *Archaias* cf. *aduncus* in the Middle East, e.g. Henson (1950), Thomas (1950, 1952), and Turnovsky (1955), refer to specimens of at least four other species but not to *A. angulatus*. One species is *Archaias kirkukensis* two more are named here *A. asmaricus* and *A. hensoni*, and the fourth is either a variety of *A. operculiniformis* or an undescribed species that occurs with it in the higher part of the Oligocene. Henson (1950) distinguished informally between *Archaias* cf. *aduncus* and *Archaias sp. 1*. In most cases his *A.* cf. *aduncus* refers to *A. hensoni* and *A. sp. 1* to *A. asmaricus*, but the diagnostic criteria are not identical and an exact correspondence cannot be maintained. The diagnoses of these species will be found below.

Occurrence. In spite of published statements, the only reliable records of the species are from Recent material from the Caribbean Sea, Gulf of Mexico, and adjacent parts of the western Atlantic Ocean. Records from other areas and fossil records should not be accepted without re-examination of material.

Archaias columbiensis Applin and Jordan 1945

Archaias columbiensis Applin and Jordan 1945, p. 141, pl. 21, fig. 6.

Remarks. The description and figures of this species, as far as they go, agree in all respects with those of *Archaias operculiniformis*, there being at present insufficient data to form a differential diagnosis. It is nevertheless probable that the two are distinct species. *A. columbiensis* seems to be the less inflated. The test is lenticular, bilaterally symmetrical, closely coiled, and has internal structures in the chambers. The chambers are involute and gently vorticiform. The probability is that the species has pillars but no subepidermal partitions, but until this is explicitly demonstrated it is not possible to decide finally if this species should remain in the genus *Archaias*.

Occurrence. Lower Middle Eocene (Lake City Limestone); Columbia county, Florida.

Archaias floridanus (Conrad 1846)

Plate 42, figs. 1, 2

Nummulites floridanus Conrad 1846, p. 399, text-fig.
N. floridanus Conrad; Heilprin 1882, p. 189.
Archaias floridanus (Conrad); Vaughan 1927 (1928), pp. 300–3, pl. 23, figs. 3*a–c*.
A. angulatus (Fichtel and Moll); Cushman 1930 (some fossil records only?), p. 46.
Puteolina (*Archaias*) *angulatus* (Fichtel and Moll); Hofker 1952, p. 463 ('microspheric form'), text-fig. 50*b*.

Description. The test is large and discoidal, fairly thick at the margin, and without a median swelling. The externally visible chambers of the last whorl are all spirally arranged, apparently with vorticiform filaments reaching the poles after more than one revolution. The last dozen chambers in fact progress from reniform to cyclical, but a characteristic radial fold that continues the line of the aduncate termination of the spire makes the whole test appear spiral on cursory examination. Vaughan records that there is 'a short

EXPLANATION OF PLATE 40

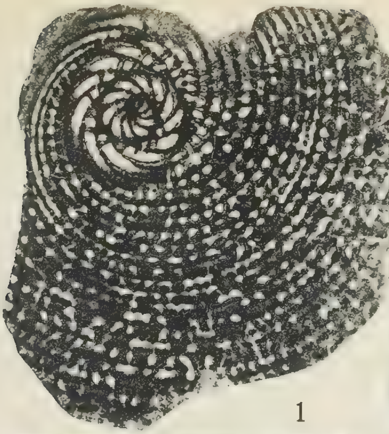
All figures magnified × 20.

Figs. 1–15. *Archaias kirkukensis* Henson 1950, Kirkuk Liwa, Iraq. 1, Nearly equatorial section showing the peripheral empty zone of the chambers where the section has passed tangentially through the earlier chambers, microspheric test. Kirkuk Well 17; Bajawan Limestone (P. 43665). 2, Equatorial section, microspheric test. Kirkuk Well 17; Bajawan Limestone (P. 43665). 3, Nearly equatorial section, megalospheric test. Kirkuk Well 17; Bajawan Limestone (P. 43665). 4, Tangential section through periphery showing the septum with apertures and interseptal pillars. Kirkuk Well 17; Bajawan Limestone (P. 43665). 5, Nearly equatorial section (after Henson). Kirkuk Well 57; Bajawan Limestone (P. 39645). 6, 7, Random sections (7 after Henson). Kirkuk Well 56; Bajawan Limestone (6—P. 43666; 7—P. 39641). 8–11, Random sections. Kirkuk Well 22; Bajawan Limestone (8, 9—P. 43667; 19—P. 43668; 11—P. 43669). 12, 13, Axial sections, megalospheric tests. Kirkuk Well 22; Bajawan Limestone (12—P. 43668; 13—P. 43670). 14, Axial section, megalospheric test. Bai Hassan Well 5; Anah Limestone (P. 43671). 15, Random section. Bai Hassan Well 5; Anah Limestone (P. 43671).

Figs. 16–20. *Archaias hensoni* sp. nov. 16, Axial section, microspheric test (after Henson). Shiranish Islam, north-east Iraq; Aquitanian (P. 39651). 17, Random section (holotype). Anah, west Iraq; ?Anah Limestone (P. 43672). 18–20, Random sections. Ain Zalah Well 1, Mosul Liwa, Iraq; Anah Limestone (18—P. 43673; 19—P. 43674; 20—P. 43675).

Figs. 21–24. *Archaias asmaricus* sp. nov. 21, 22, Random sections. Bai Hassan Well 4, Kirkuk Liwa, Iraq; Anah Limestone (21—P. 43676; 22—P. 43677). 23, Nearly axial section. Kirkuk Well 21, Iraq; Bajawan Limestone (P. 43678). 24, Nearly equatorial section. Near Anah, west Iraq; Anah Limestone (P. 43709).

Numbers in brackets are the registration numbers of the specimens/slides in the British Museum (Natural History).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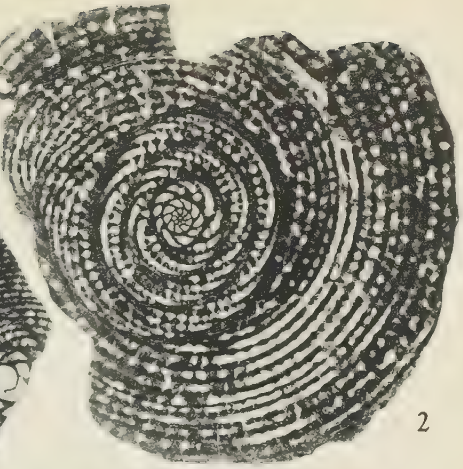
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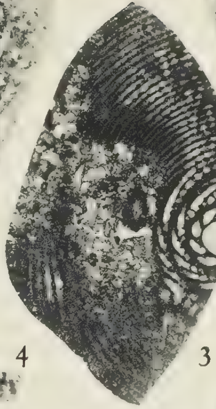
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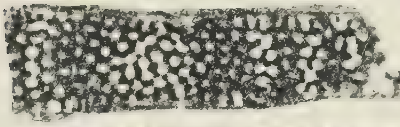
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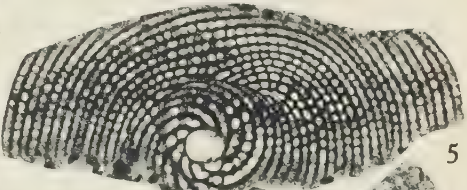
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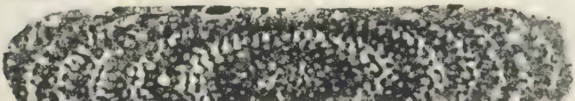
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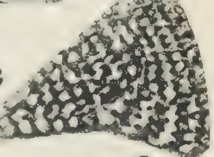
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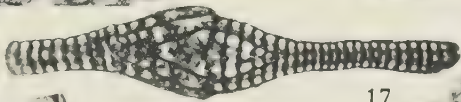
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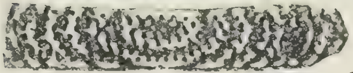
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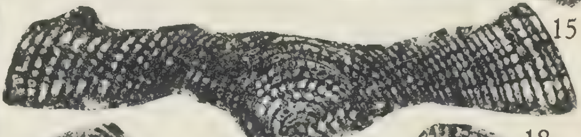
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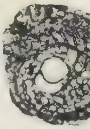
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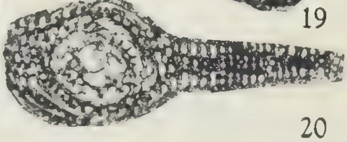
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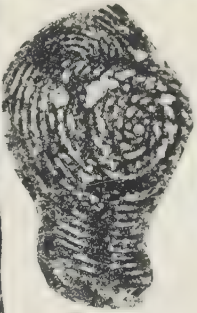
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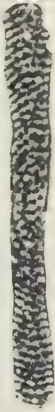
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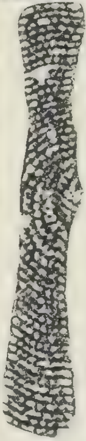
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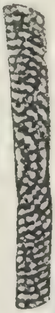
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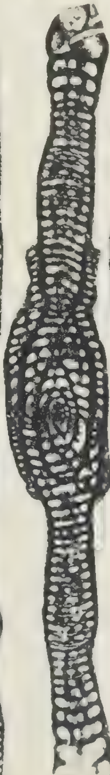
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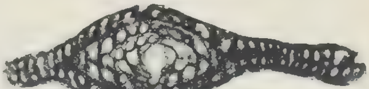
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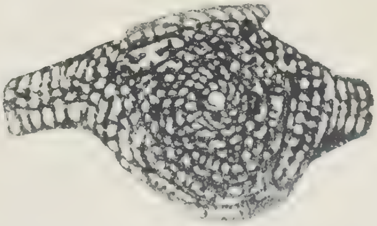
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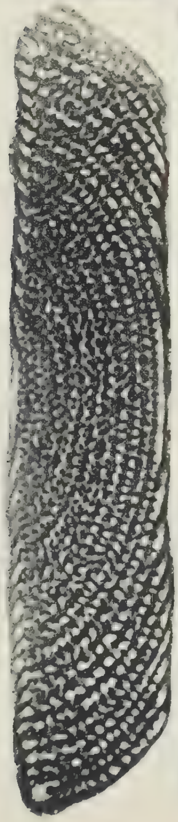
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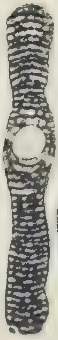
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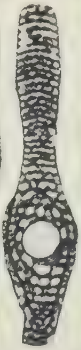
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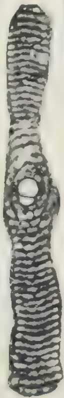
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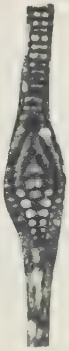
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SMOUT AND EAMES, *Archaias*

nautiloid coil of two or three turns' and 'all the large specimens sectioned were microspheric'. No further information on the structure is available, and the figured specimens are presumably microspheric.

A single British Museum specimen mounted by Lister and labelled '*Orbiculina adunca* microspheric' may be a specimen of this species. It has a different colour and texture from the other specimens of the exhibit and is probably a fossil. It shows the characteristic termination of the spire and the radial wave as in *A. floridanus.* The chambers withdraw from the poles progressively as in *A. angulatus.* The pits are the same as those of *A. angulatus.* The distance between septa is greater, agreeing with those of *A. floridanus.* There are pillars like those of *A. angulatus* and there are no subepidermal partitions. The apertures are numerous and scattered on the apertural face, which occupies all the periphery of the test.

U.S.G.S. specimen f. 3838 from the Lower Miocene of Tampa Island, Cherokee Sink, Wakulla Co., Florida shows a large specimen measuring 10 mm. × 8 mm. and about 0·8 mm. thick at the periphery. It has about six to nine cyclical chambers and several reniform ones, the spire not being visible. The reniform chambers have alar prolongations but the number of degrees that they originally subtended cannot now be seen. The alar prolongations are so related to the earlier whorls that the test is discoidal with little or no polar swelling. The radius of the test at the beginning of the cyclical stage is at least 1·5 mm. The later chambers have nine rows of pillars; they are irregularly arranged, anastomose slightly, and are smaller at the sides of the chamber than in the central region. Subepidermal partitions are absent. Many other specimens of Peneroplidae are present in the same rock but all seem to belong to other species. It is highly probable that both of the above specimens are the same species and correctly identified as *Archaias floridanus.* The British Museum specimen seems to terminate while the test is still spiral, but the Smithsonian one shows the development of a cyclical stage which still has a reniform shape; they both show the kink so typical of *A. floridanus*; in the reniform and cyclical stages the spiral line is continued by a sharp inflexion of the margin.

Dimensions

Maximum diameter 12·25 mm.; most specimens measure 10 mm. or less.
Thirty-three chambers in 4·5 mm. radius.

Remarks. Archaias floridanus appears to be a species quite distinct from *A. angulatus,* from which it is easily distinguished by the more discoidal shape, the radial wave and the associated kink in the margin, the development of a terminal cyclical stage, and the chamber spacing. Its attribution to the genus *Archaias* is supported by the new evidence.

Occurrence. Lower Miocene Tampa Formation of Florida. Fossil occurrences of *Archaias spp.* from the Miocene of Panama and the West Indies may be this species but further observation of the material is required before this species can be separated from fossil records of *A. angulatus. A. floridanus* has not been found in Recent material.

Archaias operculiniformis Henson 1950

Plate 39, figs. 6–9

Archaias operculiniformis Henson 1950, p. 44, pl. 7, figs. 5, 6.
A. operculiniformis Henson; Thomas 1950, pp. 38, 40.

A. operculiniformis Henson; Kent, Slinger, and Thomas 1951, p. 11.
A. operculiniformis Henson; Thomas 1952, p. 75.
A. operculiniformis Henson; Grimsdale 1952, p. 224.
A. operculiniformis Henson; Turnovsky 1955, pp. 160–1.
A. operculiniformis Henson; Van Bellen 1956, p. 250, pl. 2, fig. *d*.

Description. The test is lenticular with a subacute margin. The spire is comparatively laxly coiled and shows less subdivision into a central, tightly coiled portion and terminal flange than in most species of *Archaias*. The terminal flare shows no recurvature and is therefore not aduncate. The chambers are equitant and probably completely involute throughout. The numerous septa are curved, but less so than is usual in *Archaias*, and the septa therefore never subtend more than a quadrant each. The alar prolongations are gently vorticiform. The epidermis is very thick. The chambers are crowded with interseptal pillars, which are also to be found in the alar prolongations. The species is dimorphic, but not strikingly so. The last few chambers (about four) are brood chambers in the microspheric form and are double the usual height, with much reduced pillars. The megalosphere is small and spherical, with a short neck-chamber which has its distal end swollen. The characters of the earliest chambers are not well known. The apertures are scattered on the apertural face.

EXPLANATION OF PLATE 41

All figures magnified × 30.

Gach Saran Wells 6 and 11, Iran; Middle Asmari Limestone (Aquitanian). Figs. 1–25 from Well 6, numbered mainly in descending stratigraphical sequence; figs. 26–37 from Well 11, numbered mainly in descending stratigraphical sequence.

Figs. 1–5. *Archaias hensoni* sp. nov.; Well 6. 1, depth 3,685 ft., 49 ft. below top of Middle Asmari Limestone (P. 43679). 2, depth 3,701 ft. (P. 43680). 3, depth 3,717 ft. (P. 43681). 4, 5, depth 3,747 ft. (P. 43682).

Figs. 6–8. *Archaias asmaricus* sp. nov.; Well 6. 6, depth 3,846 ft. (P. 43683). 7, holotype, depth 3,844 ft. (P. 43684). 8, depth 3,846 ft. (P. 43685).

Fig. 9. *Archaias sp.*; Well 6, depth 3,847 ft. (P. 43686).

Fig. 10. *Archaias asmaricus* sp. nov.; Well 6, depth 3,847 ft. (P. 43687).

Fig. 11. *Archaias sp.*; Well 6, depth 3,850 ft. (P. 43688).

Figs. 12–19. *Archaias kirkukensis* Henson; Well 6. 12, depth 4,021 ft. (P. 43689). 13, depth 4,120 ft. (P. 43690). 14, 15, depth 4,117 ft. (P. 43691). 16, 17, depth 4,127 ft. (P. 43692). 18, 19, depth 4,130 ft. (P. 43693).

Fig. 20. *Archaias asmaricus* sp. nov.; Well 6, depth 4,130 ft. (P. 43693).

Fig. 21. *Archaias hensoni* sp. nov.; Well 6, depth 4,134 ft. (P. 43694).

Figs. 22–25. *Archaias kirkukensis* Henson; Well 6. 22–24, depth 4,134 ft. (P. 43694). 25, depth 4,143 ft., 117 ft. above base of Middle Asmari Limestone (P. 43695).

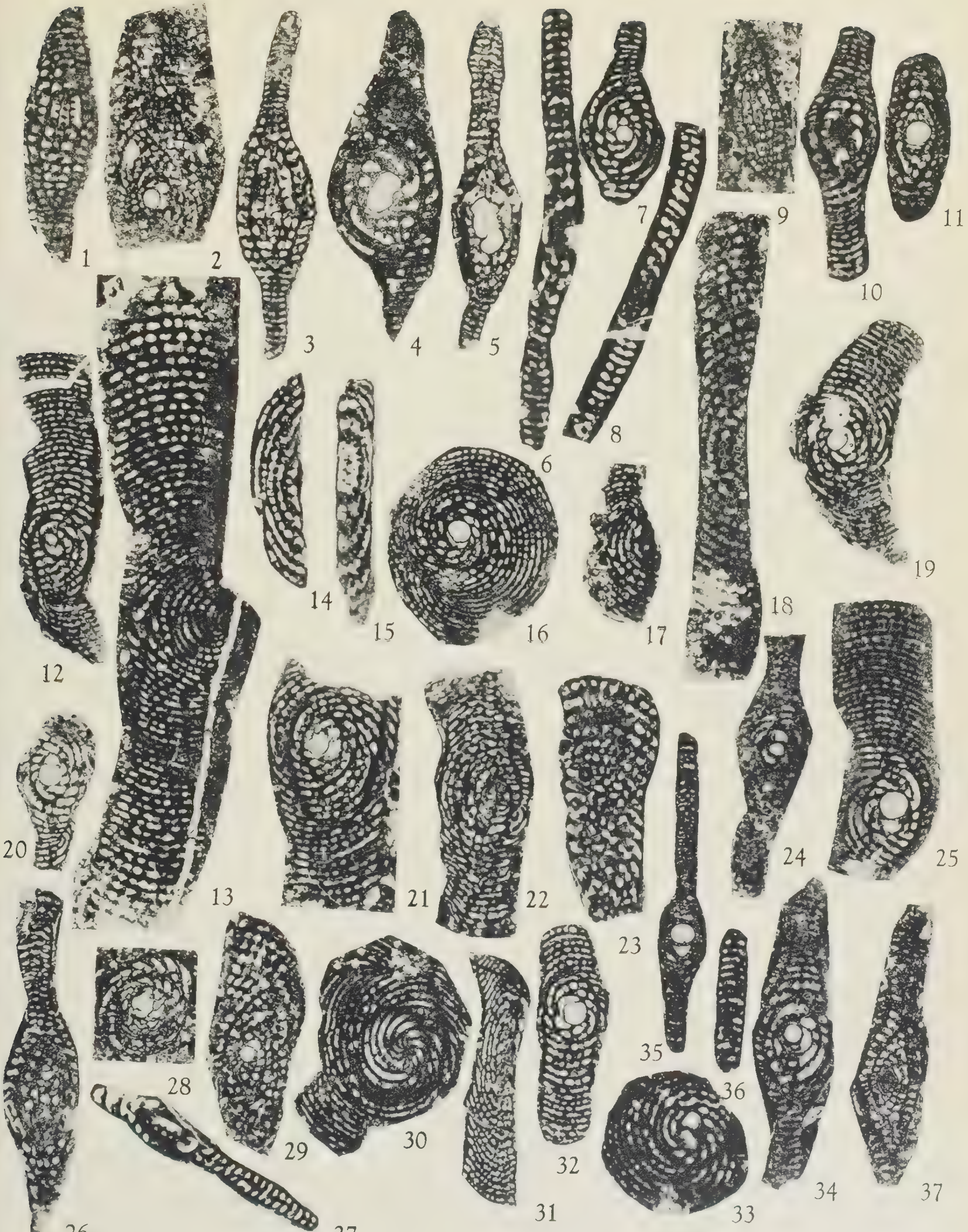
Fig. 26. *Archaias hensoni* sp. nov.; Well 11, depth 5,500 ft., 115 ft. below top of Middle Asmari Limestone (P. 43696).

Fig. 27. *Archaias asmaricus* sp. nov.; Well 11, depth 5,586 ft. (P. 43697).

Figs. 28–29. *Archaias hensoni* sp. nov.; Well 11, depth 5,632 ft. (P. 43698).

Figs. 30–37. *Archaias kirkukensis* Henson; Well 11. 30, depth 5,682 ft. (P. 43699). 31, depth 5,811 ft. (P. 43700). 32, depth 5,802 ft. (P. 43701). 33, depth 5,895 ft. (P. 43702). 34, depth 5,992 ft. (P. 43703). 35–36, depth 6,045 ft. (P. 43704). 37, depth 6,107 ft., 43 ft. above base of Middle Asmari Limestone (P. 43705).

Numbers in brackets are the registration numbers of specimens/slides in the British Museum (Natural History).



SMOUT AND EAMES, *Archaias*

Dimensions

Microspheric test: Maximum diameter 3·6 mm.

Whorl no.	1	2	3	4	5	6
Septa	?	?	27	26	34	34+

Septa spaced about 0·06 to 0·09 mm.
About four brood chambers.

Megalospheric test: Maximum diameter 2·6 mm.
Thickness at poles 1·0 to 1·5 mm.
Diameter of proloculus 0·17 mm.
Diameter of nucleoconch 0·28 mm.

Whorl no.	1	2	3	4
Septa	?	?	?	40?

Remarks. The lenticular shape, the lack of a cyclical or flabelliform stage, and the rudimentary development of the terminal flange distinguish this from all known species of *Archaias* except *A. columbiensis*. The terminal flare is so short and the chambers so little recurved that no axial section will show it on both sides of the test. The details of the chambers and pillars are such that fragments cannot always be distinguished from those of *A. hensoni*, &c. The specimens illustrated on Pl. 39, figs. 10, 11 show the difficulty. Fig. 10 was called *Archaias sp. 1* by Henson (1950). It is not certain that it is *A. operculiniformis*, and it might be *A. hensoni* or an undescribed species. There is no satisfactory known difference between *A. operculiniformis* and *A. columbiensis*, but in view of the different geological age and the wide geographical separation it is not likely that the species are synonymous.

Occurrence. Oligocene Khamir limestone and Lower Asmari limestone of Iran, Shurau Limestone of Iraq; Lattorfian?, Rupelian, Chattian.

This species was originally described from the Oligocene part of the Khamir limestone of south-west Iran. Thomas (1950, 1952) recorded it in the Asmari limestone. In Iraq the species occurs commonly in the shoreward part of the Shurau limestone with a fauna that includes *Austrotrillina paucialveolata* Grimsdale 1952, *Peneroplis glynnjonesi* Henson 1950, *Quinqueloculina spp. P.* cf. *evolutus* Henson 1950, and *Heterillina hensoni*, cf. Van Bellen 1956. In Iran, in Gach Saran Wells 6 and 11, we find *A. operculiniformis* in a miliolite intercalated between forereef type limestones of the Lower Asmari Limestone with *Nummulites intermedius* (d'Archiac) 1846 above and below but with *Lepidocyclina* above only. The accompanying fauna of the miliolite includes *Austrotrillina sp.* (not easily distinguished from *A. paucialveolata* or *A. howchini* and presumably intermediate in character), *Peneroplis thomasi* Henson 1950, *P. evolutus* Henson, *Praerhapydionina delicata* Henson, and *Bullalveolina bulloides* (d'Orbigny) 1826. A single occurrence at the top of the Lower Asmari Limestone in Gach Saran Well 6 suggests survival of *A. operculiniformis* into the Chattian, i.e. above the range of *Nummulites intermedius*. *Archaias* cf. *aduncus* with *A. operculiniformis* is recorded by Thomas (1950) from Tang-i-Gurgurda, near Gach Saran. These specimens may be from the same bed as that at the top of the Lower Asmari Limestone seen in Gach Saran Well 6, where a proportion of the specimens cannot be identified specially and may not be *A. operculiniformis*. The Shurau limestone resembles the band that carries the main occurrence of *A. operculiniformis* in Gach Saran; the Sheikh Alas limestone below contains *Nummulites intermedius*, and the Baba limestone above, *N. intermedius* and *Lepidocyclina spp.*

Archaias kirkukensis Henson 1950

Plate 40, figs. 1–15; Plate 41, figs. 12–19, 22–25, 30–37

Archaias kirkukensis Henson 1950, p. 43, pl. 7, figs. 3, 4, 9, pl. 8, figs. 1–5.
A. kirkukensis Henson; Turnovsky 1955, p. 156.
A. kirkukensis Henson; Van Bellen 1956, p. 250, fig. 1*a*.

Description. The test is discoidal to biconcave and has a central boss only in the very early stages of growth. The microspheric form has a spire of about 5½ whorls and the megalospheric of about one whorl, in both cases ending in a terminal flare with only a trace of aduncate recurvature. This is followed by a reniform stage of about seven chambers, succeeded by cyclical chambers forming about half the diameter, or more, of the test. The earlier spiral chambers are involute; it is not known how the transition to the evolute cyclical stage is effected but probably it is abrupt. The reniform stage does not make a strong nick in the margin and it is soon abolished by later cyclical chambers. The spiral chambers are strongly curved; the apertural face occupies most of the margin before the test has attained a quarter of its final diameter. The chambers are mostly filled with crowded pillars, which may form up to six rows in the later chambers, but the pillars leave narrow lateral empty zones and are sparse in the alar prolongations of the spiral chambers. In the first three whorls of the microspheric test and the first one or two chambers of the megalospheric test there may be no pillars and the immediately succeeding chambers may have only a single row of pillars per chamber. The apertural face is densely crowded with apertural pores, about seven across in the largest chambers, but not arranged in rows. Brood chambers have never been found. The epidermis is thin. The megalosphere is spherical; the neck chamber subtends about 100° and is usually in the equatorial plane. It is uncertain if this species is trimorphic; apparently small megalospheres may be inaccurately equatorial sections.

Dimensions

Microspheric test: Maximum diameter of test 9 mm.
Maximum thickness of test (margin) 1·1 mm., often less.
Reniform stage begins at about 1·7 mm. diameter.

Whorl no.	1	2	3	4	5	6	Reniform	Cyclical
Septa	9	9	10	11	12	13	7	20

The septa are usually about 0·07 mm. apart but may be more than 0·1 mm. apart (14 to 20 per mm.).

Megalospheric test: Maximum diameter of test 3 mm.
Maximum thickness of test 0·3 mm. (poles and margin).
Minimum thickness of test 0·2 mm. (at beginning of cyclical stage).
Reniform stage begins at 0·6 to 1·0 mm. diameter, not 0·33 mm. as stated by Henson.

Whorl no.	1	2	Reniform	Cyclical
Septa	9	9	9	14

Septa about 0·07 mm. apart (14 per mm.).
Diameter of megalosphere 0·18 to 0·24 mm.
Maximum diameter of nucleoconch 0·26 mm. to 0·35 mm.

Remarks. This species is unusual in having a very short spiral stage, which appears longer than it really is in axial section because the alar prolongations of the chambers are strongly vorticiform. It has a large cyclical disk, only very few specimens showing a polar swelling. The cyclical development and discoidal shape distinguish it from *A. operculiniformis*. The species *A. angulatus*, *A. asmaricus*, and *A. hensoni* have substantial polar swellings that only very rarely are reduced to the size of the most swollen specimens of *A. kirkukensis*. The spiral stage of all these species is larger, with more whorls than in *A. kirkukensis*. *A. asmaricus* is further distinguished by the single equatorial row of pillars and the thicker epidermis.

All the diagnostic characters are difficult to observe in random thin sections. The most useful practical diagnosis is the rarity of any visible central boss in random section, and the complete absence of any substantial lenticular development.

Occurrence. Middle Asmari Limestone (Aquitanian) of Iran. Bajawan and ? Anah Limestone of Iraq.

Archaias hensoni sp. nov.

Plate 40, figs. 16–20; Plate 41, figs. 1–5, 21, 26, 28, 29

Archaias cf. *aduncus* Henson 1950 (*pars*), p. 44, pl. 8, figs. 6, 7.
Archaias cf. *aduncus* Thomas 1952 (*pars*), p. 75.

Description. The test is discoidal, with a narrow flange and a swollen central boss that occupies about half of the diameter. It is probable that the test terminates at the end of the spiral stage. A few reniform or cyclical chambers might be produced, but good equatorial sections have not been seen, nor have whole specimens which are not totally embedded in rock been found. There is little difference between the megalospheric form of this species and that of *A. asmaricus* except that the flange is slightly thicker and there is more than one row of pillars in the later chambers. This makes the resemblance to *Peneroplis thomasi* much less than is the case with *A. asmaricus*, but the thick epidermis seems still to be present. The spire is probably different, but direct comparison is impossible with existing specimens. The megalospheric form has at least five whorls and two brood-chambers.

A new specific name is considered justified by the present additional information, which enables practical distinction of the species from *A. kirkukensis* and *A. asmaricus*. *A. floridanus* is more robust, has more numerous pillars, and has even more vorticiform alar prolongations of the chambers. *Archaias angulatus* also has a more robust flange and much more numerous pillars; its epidermis is thin. The termination of the spire of *A. hensoni* is unknown, but it is most unlikely that it has the exaggerated aduncate flare of *A. angulatus*. In random sections there is a preponderance of specimens showing a thin disk and substantial median swelling, contrasting with the thick disk without median swelling of *A. kirkukensis*, Distinction from *A. asmaricus* depends on determining the number of rows of pillars in the later chambers. The latter species shows a proportion of random sections cut obliquely and making one row of pillars look like two or three, but always includes sections in which the single row is clearly present.

Dimensions

Microspheric test: Maximum diameter 5·1 mm.
Thickness at poles 0·7 mm.
Thickness of flange 0·28 mm.

Distance between septa centres 0·05 mm. increasing to 0·1 mm.
About two brood-chambers of double height.
Up to three rows of pillars per chamber.

Megalospheric test: Maximum diameter 2·7 mm.
Thickness at poles (true) about 0·3 mm.
Thickness at poles (apparent) 0·8 to 0·4 mm.
Thickness of flange 0·15 mm.
Diameter of proloculus 0·12 mm.
Maximum diameter of nucleoconch 0·22 mm.
Distance between septa centres about 0·05 mm.
Up to three rows of pillars per chamber.

Occurrence. Middle Asmari Limestone (Aquitanian) of Iran. Anah and ? Bajawan Limestone of Iraq.

Remarks. This species, although including most of the specimens of *Archaias* cf. *aduncus* Henson 1950 and Thomas 1952, is not identical in definition. Owing to the lack of hand specimens no complete description of this species can be given, but it is recognizably distinct from other species on comparative characters.

Archaias asmaricus sp. nov.

Plate 40, figs. 21–24; Plate 41, figs. 6–8, 10, 20, 27

Archaias sp. 1 Henson 1950 (*pars*), p. 45, pl. 7, figs. 7, 8.

Description. The test has a thin flange with a stout, lenticular, median swelling occupying up to half or more of the diameter of the test. The test closely resembles that of *Peneroplis thomasi*, and can only be distinguished with certainty if the pillars can be seen; even the thick epidermis is a feature in common. The interseptal pillars are distinctive in being restricted to a single row in the equatorial plane. These are well seen in axial section, in which the pillaring, external shape, and thick epidermis give a very striking appearance that cannot be mistaken for any other species. Strictly equatorial sections will cut all the pillars and cannot be easily distinguished from *A. kirkukensis* or *A. hensoni*. Sections parallel to the equatorial plane will not show pillars and will be absolutely identical with similar sections of *P. thomasi*. Oblique sections will appear to show several rows of pillars per chamber. The microscopic spire is probably of about four whorls, and it is probable that the flange consists of reniform chambers followed by a few cyclical ones, as in *P. thomasi*. All chambers are involute and strongly curved until the cyclical stage, which must be evolute. The megalosphere is small, and is followed by a neck-chamber of about 100°, swollen distally. The spire is of about two whorls but the vorticiform alar prolongations can make it appear more in axial section.

Dimensions

Microspheric test: Maximum diameter 3·5 mm.
Thickness of flange about 0·2 mm.
Distance between the centres of septa 0·05 mm.

Megalospheric test: Maximum diameter 2 mm.?
Maximum thickness at poles 0·6 mm.?

Distance between centres of septa 0·05 mm.
Maximum diameter of proloculus 0·16 mm.
Maximum diameter of nucleoconch 0·20 mm.?

Remarks. A. asmaricus is distinguished from all other species of *Archaias* by the restriction of the interseptal pillars to a single row in the equatorial plane. They tend to be continuous from chamber to chamber, but occasionally the position of the row will shift abruptly, and often it shifts progressively. The single row of pillars will be mistaken for a double or a triple row if an oblique section is mistaken for an axial one, and an accurately equatorial section can show as many pillars as any other species. Usually, sections are not so accurate, and lack of pillars laterally can be observed. There has been, however, a tendency to misdetermine specimens as *A. hensoni*, although the two species are really distinct. The general similarity to *Peneroplis thomasi* is striking except in nearly equatorial section, where the similarity is obscured by the pillaring; this similarity is so close that sections which fail to cut the equatorial plane cannot be distinguished from those of *P. thomasi* by any means. This suggests that *A. asmaricus* evolved from *P. thomasi* in Aquitanian times and that the genus *Archaias* is consequently polyphyletic.

Henson (1950) in defining *Archaias sp. 1* emphasized the occasional alignment of pillars in successive chambers. This character is often seen in *A. asmaricus* but is not used diagnostically.

Occurrence. Middle Asmari Limestone (Aquitanian) of Iran. Bajawan and Anah Limestones of Iraq.

SPECIES NOMINALLY PLACED IN *ARCHAIAS* BY SOME AUTHORS BUT NOT ACTUALLY BELONGING TO THIS GENUS

'*Archaias*' *rotella* (d'Orbigny) 1846

Orbiculina rotella d'Orbigny 1846, p. 142, pl. 7, figs. 13, 14.

Remarks: This species is only nominally retained under the name *Archaias*, of which *Orbiculina* is a synonym. The structure appears to be that of *Borelis* or some related genus of the Alveolinellidae. The lenticular shape is unusual, but it is not unprecedented in that family.

Archaias vandervlerki de Neve 1947

Archaias vandervlerki de Neve 1947, pp. 14–16, figs. 1–4.
Archaias vandervlerki de Neve; Cole 1957*b*, p. 335, pl. 103, figs. 5–9.

Remarks: This species is incompletely described and therefore cannot be placed with complete confidence. It is highly probable that it is *Orbitolites malabarica* Carter 1853, regarded as a *Taberina* by Henson 1950, and distinguished from *Archaias* by the presence of subepidermal partitions in addition to interseptal pillars.

Occurrence: Lower Miocene Poelobalang Beds of Borneo; Lower Miocene of Java and Saipen.

Cyclorbiculina compressa (d'Orbigny) 1839

Orbiculina compressa d'Orbigny 1839, p. 66, pl. 8, figs. 4–7.
O. adunca (Fichtel and Moll); Brady 1884 (*pars*), pp. 62, 132, 208–9.
Orbiculina adunca (Fichtel and Moll); Flint 1899 (*pars*), p. 304, pl. 50, fig. 1 (*pars*).
O. adunca (Fichtel and Moll); Lister 1903 (*pars*), pp. 95, 143.
O. adunca var. *flabelliformis* Lister 1903, pp. 96–97, text-figs. 30*c–e*.
O. compressa d'Orbigny; Cushman 1919, p. 70, pl. 7, fig. 6.
O. compressa d'Orbigny; Cushman 1922, p. 81.
O. compressa d'Orbigny; Cushman 1925, pl. 16, fig. 2.
Archaias compressus (d'Orbigny); Cushman 1930, p. 48, pl. 17, figs. 1, 2.
A. compressus (d'Orbigny); Hofker 1930, pp. 143–7.
Cyclorbiculina compressa (d'Orbigny); Silvestri 1937, p. 88.
Puteolina (*Archaias*) *compressa* (d'Orbigny); Hofker 1952*a*, pp. 457–60, figs. 44–48.
Archaias compressus (d'Orbigny); Cole 1957*a*, p. 328, pl. 24, figs. 1–9.

Remarks. This species is very distinct from *Archaias angulatus* although it occurs with it and has been extensively confused with it. Subepidermal partitions can be seen very clearly and in some cases there seems to be a central zone with pillars. The spire is smaller than that of *A. angulatus* and as a result the later chambers are cyclical or flabelliform. The early chambers are involute but the flabelliform and cyclical stages are evolute. Other specific differences are given by Hofker 1952*a*. There is no possibility that the two species intergrade. *C. compressa* has previously been included in *Archaias*, but Henson's revision of the genus excludes it. Silvestri proposed the monotypic genus *Cyclorbiculina* for it.

Occurrence. The Caribbean Sea, Gulf of Mexico, and adjacent parts of the western Atlantic. Later Tertiary fossil records in this area are mentioned by Cushman 1930, but we are unable to express an opinion on their correctness. Cole (1957*a*) figured specimens from the Bohio and Caimito formations of Panama, of 'late Oligocene' age (in our opinion the age is Aquitanian).

Orbitolites malabarica Carter 1853

Orbitolites malabarica Carter 1853, p. 425, pl. 16*b*, figs. 1–4.
O. malabarica Carter; Carter 1857, pp. 630, 634–5.
Orbiculina malabarica (Carter); ibid., p. 634.
O. sp. Carpenter 1856, pp. 549, 552.
O. malabarica (Carter); Douvillé 1902, pp. 299–301, 305.
O. malabarica (Carter); Wayland and Morley Davies 1923, pp. 577–602.
Archaias malabarica (Carter); Vaughan 1928 (1927), p. 302.
A. vandervlerki de Neve 1947, p. 14, pl. 15, figs. 1–4.
Taberina malabarica (Carter); Henson 1950, p. 50, pl. 3, figs. 7, 11, 12.
T. malabarica (Carter); Eames 1950, pp. 233–52.
T. malabarica (Carter); Mohan and Chatterji 1956, pp. 349–56, text-figs. 1–3.
Archaias vandervlecki de Neve; Cole 1957*b*, p. 328, pl. 103, figs. 5–9.

Remarks. Henson 1950 demonstrated that this species cannot belong to the genus *Archaias* because the chambers have both interseptal pillars and subepidermal partitions. Whether it is correctly determined as a species of *Taberina* is doubtful, for the type species of that genus is incompletely described. *T. malabarica* has not been found in Iraq or in any of the Asmari limestone samples from Iran that we have examined.

Orbiculina mamillata Carter 1857

Orbiculina mamillata Carter 1857, p. 593.

Remarks. Since *Orbiculina* is a synonym of *Archaias*, this species must be added nominally to the list. The type figure leaves little doubt that it is really a species of *Orbitolina* auctt. *non* d'Orbigny 1850 (*Orbitolinopsis*?). It is too incompletely described and figured for precise identification.

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AN EOCENE SEA-PEN FROM DUNEDIN, NEW ZEALAND

by D. HAMILTON

ABSTRACT. A new Upper Eocene pennatulid from the Burnside Mudstone, Dunedin, New Zealand, is described and named *Bensonularia spatulata*. It is assigned to the Family Veretillidae.

THIS is the first record of a pennatulid to be collected from Tertiary marine strata in New Zealand. The specimen was collected by the writer from a calcareous mudstone, the Burnside Mudstone, in the quarry operated by the Milburn Lime and Cement Co., Ltd., Burnside, Dunedin. Specimens of fossil pennatulids are relatively rare owing mainly to their delicate structure and the hazards of preservation. The Burnside specimen, however, consists of an almost complete rachis and is remarkably well preserved (Pl. 42, fig. 3). Bayer (1956, p. F224 et seq.) includes eleven families in the Suborder Sessiliflorae of the Pennatulacea, and the only fossil representatives of this suborder previously recognized are placed in the Family Renillidae. These forms show bilateral symmetry. The Burnside specimen lacks bilateral symmetry, so that it represents the most primitive evolutionary stage yet found in the fossil record.

Phylum COELENTERATA
Class ANTHOZOA
Subclass OCTOCORALLIA
Order PENNATULACEA Verrill 1865
Suborder SESSILIFLORAE Kükenthal 1915
Family VERETILLIDAE Herklots 1858
Genus BENSONULARIA gen. nov.

Type species *Bensonularia spatulata* gen. et sp. nov.

Diagnosis. Well-developed colony, compressed, but without bilateral symmetry, bearing zooids regularly arranged in sinistral and dextral spirals over the surface of the rachis. No calices. Spicules of the rachis are spindle-shaped.

Discussion. The compressed spatulate rachis of the specimen suggests an incipient bilateral symmetry, but the symmetry of the colony is dominantly radial as in the primitive Family Veretillidae. The zooids are arranged in a double spiral over the rachis, and this represents a considerable advance in symmetry over the irregular distribution of the zooids on the rachis so commonly found in the Family Veretillidae. This double spiral arrangement, however, is more primitive than the transverse rows of zooids characteristic of the Family Echinoptilidae. In that family incipient bilateral symmetry is shown by the trace of a groove or track on the rachis, and this groove is free of autozooids (Hickson 1918, p. 118). There is no trace of a groove on the surface of *Bensonularia*.

The spicules of the rachis of *Bensonularia* are constant both in form (i.e. spindles) and size (about 1 cm. long), as far as can be determined from the specimen. This constancy of spicule form contrasts with most of the sea-pens placed in the Family Vere-

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tillidae. The primitive Veretillids show great variability in spicule shape and size, even between specimens of the same species collected from a similar locality (Hickson 1918, p. 126). The same author points out (1918, p. 123) that the spicules in the more advanced bilaterally symmetrical pennatulids 'are constantly of the same form and approximately of the same size'.

Though the arrangement of the zooids and the regular spicule form are comparatively advanced characters, these features are associated with radial symmetry only, so that *Bensonularia* is placed in the Family Veretillidae.

If *Bensonularia* is truly an advanced Veretillid, then the occurrence of an axis becomes at least probable. Hickson (1918, p. 119) points out that the occurrence of an axis in forms assigned to the Family Veretillidae is very variable, but in the higher forms, with stronger muscles to meet the needs of a free colony, the axis becomes a more constant feature. As the colony of *Bensonularia spatula* is large and in some respects advanced, it seems probable that an axis, possibly incomplete, was present in the living form.

The genus is named after the late Professor-Emeritus W. N. Benson, as a tribute to his contribution to the palaeontology and stratigraphy of the Dunedin district.

Bensonularia spatulata sp. nov.

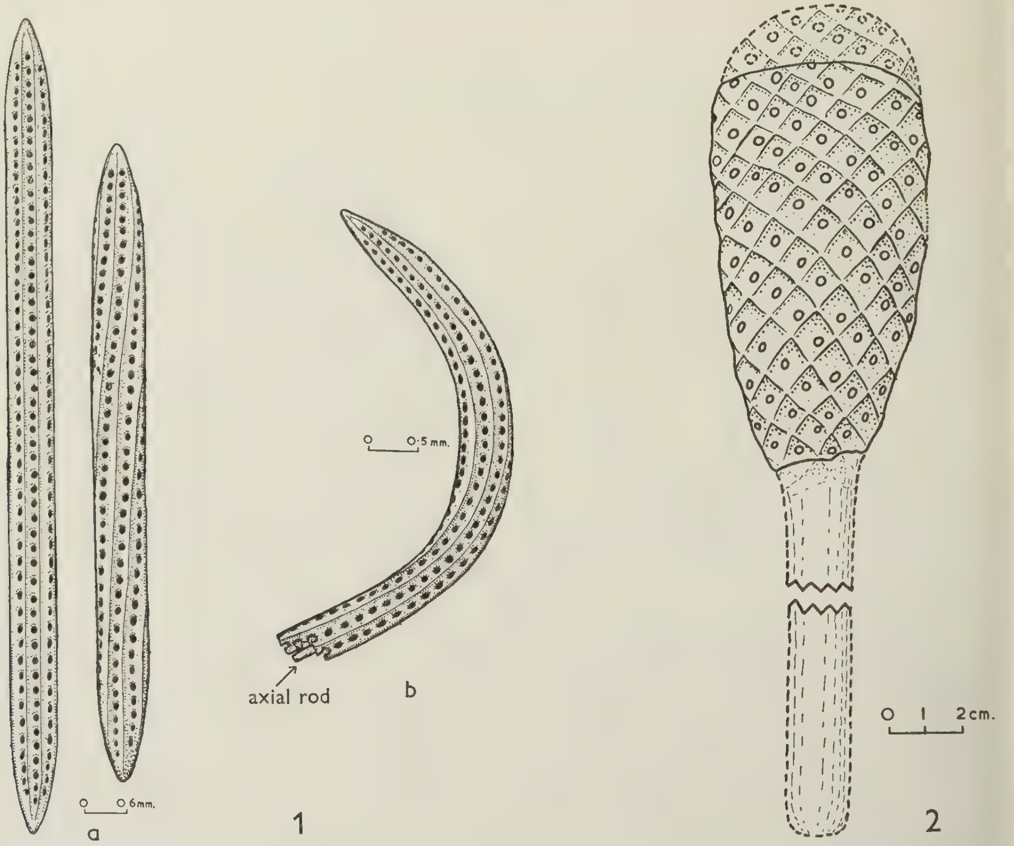
Plate 42, figs. 3, 4

Holotype. O.U. 5846. Specimen from Burnside Mudstone, Bortonian Stage (Upper Eocene), Burnside, Dunedin, New Zealand. In the Geology Department, University of Otago.

Diagnosis. Well-developed colony, compressed and spatulate in form. Zooids arranged in ascending sinistral and dextral spirals over the whole surface of the rachis. Zooid spirals separated by low ridges, which, on crossing, form diamond-shaped areas on the rachis. A single zooid occurs in each diamond-shaped area. Spicules are spindle-shaped, thickly pointed at each end, with six low hyaline ridges running the full length of the spicule, often in a slightly dextral spiral (text-fig. 1*a*). Between these hyaline ridges are single longitudinal rows of deep pits, which penetrate to a central axial rod in the spicule. Spicules of the coenenchyme lie parallel to the outer surface, interwoven, but with the longer spicules arranged longitudinally (Pl. 42, fig. 4).

Description. The specimen is preserved in a homogeneous, light-grey, calcareous mudstone matrix, and the filling of the gastric cavity is of the same lithology. The specimen (Pl. 42, fig. 3) consists of the major portion of the rachis and the mould of one side. The rachis is compressed. As other delicate fossils in the Burnside Mudstone show only slight or no distortion, it is probable that the preserved shape is that of the living colony. This interpretation is supported by the fact that the spicular arrangement on the specimen shows only slight signs of distortion along the flattened margins.

The precise nature of the spicules is rather difficult to determine, for, like some other calcareous remains in the Burnside Mudstone, they have been converted almost completely to marcasite and pyrite. However, fragmentary portions show an outer hyaline calcite layer with the six hyaline longitudinal ribs and also the pointed ends of the spicules. The fine mudstone matrix faithfully preserves the moulds, which clearly show the single row of pits between the ribs. Reconstructions of two rachis spicules are shown in text-fig. 1*a*. The structure is best shown by a partly altered C-shaped spicule taken from the supporting bundle around a zooid pore (text-fig. 1*b*). The broken end of the spicule reveals the pits penetrating to the central axial rod.



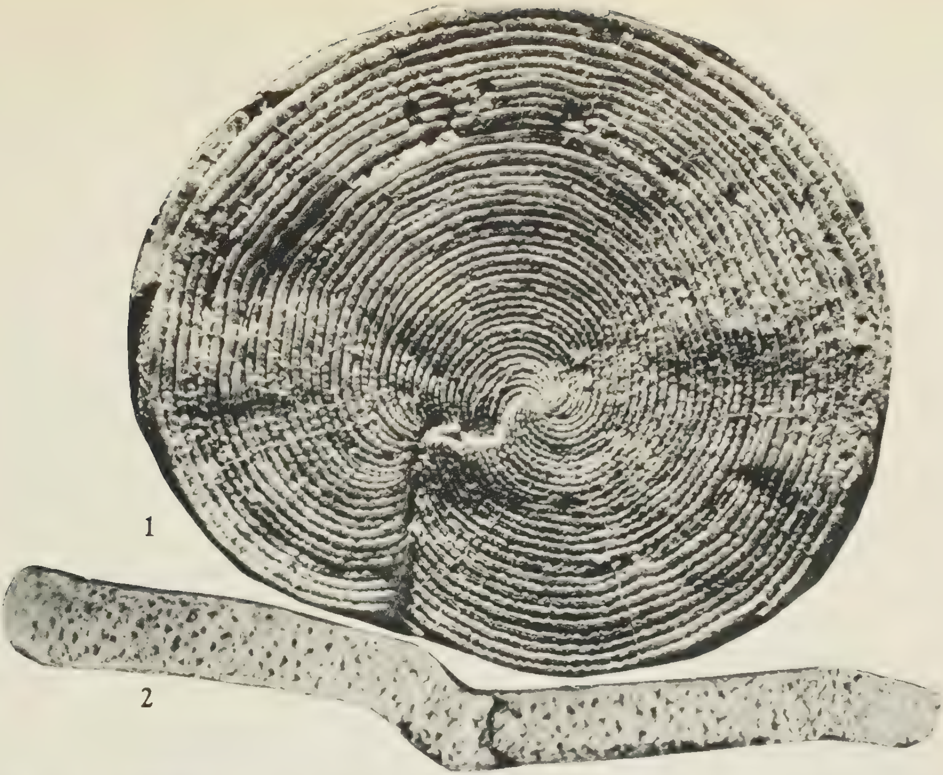
TEXT-FIGS. 1, 2. *Bensonularia spatulata* gen. et sp. nov. 1*a*, Spicules of the rachis. 1*b*, Scaphoid spicule from supporting bundle; broken end shows central axial rod. 2, Reconstruction.

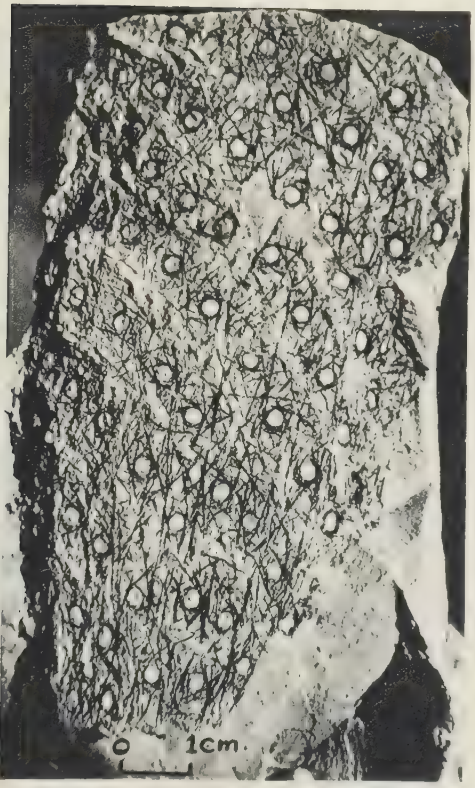
Though Recent pennatulids invariably have dimorphic zooids, the pores on *Bensonularia spatulata* are all about 3 mm. in diameter. It is therefore not possible to distinguish between the distribution of the autozooids and siphonozooids on the rachis. The ridges separating the zooid spirals are low, and on the specimen the dextral spiral ridges are only weakly developed.

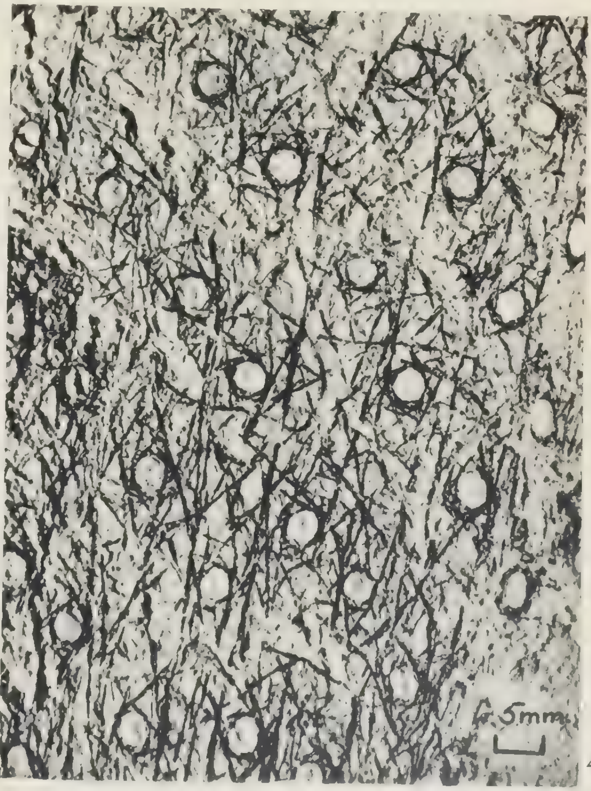
EXPLANATION OF PLATE 42

Figs. 1 and 2. *Archaias floridanus* (Conrad), Lower Miocene Tampa Formation, Tampa Island, Cherokee Sink, Wakulla County, Florida, U.S.A.; U.S.G.S. specimen f. 3838. 1, Shows the decorticated lateral surface; × 10. 2, The margin with the radial wave; × 15.

Figs. 3 and 4. *Bensonularia spatula* gen. et sp. nov., Eocene, Dunedin, New Zealand. 3, Shows the double spiral arrangement of the zooids and ridges on the rachis. 4, The spicular arrangement; note the longitudinal alignment of the long spicules.







SMOUT AND EAMES, *Archaias*
HAMILTON, Sea-Pen from New Zealand

Unfortunately the specimen is broken at both ends, so that the complete morphology of the colony is not known. However, the specimen does show a rounding towards the distal end and the rachis tapers regularly towards the proximal end, suggesting a smooth mergence of the rachis and stalk. A hypothetical reconstruction is shown in text-fig. 2.

In spite of the delicate preservation the broken ends of the specimen reveal no trace of an axis nor of any subdivision of the gastric cavity.

Measurements

Length of specimen	107 mm.
Maximum width	62 mm.
Minimum width	31 mm.
Distal section of broken end	58 mm. by 19 mm.
Proximal section of broken end	31 mm. by 10 mm. (approx.)
Diameter of zooid pores	3 mm.
Linear spacing of zooid pores	6 mm. to 12 mm.
Height of surface ridges	2 mm. to 3 mm.
Length of spicules	5 mm. to 15 mm.
Diameter of spicules	0·3 mm. to 0·6 mm.
Thickness of coenenchyme	5 mm.

From these measurements it is seen that *Bensonularia spatulata* is an unusually large pennatulid, and the spicules are also larger than those commonly present in this order.

Palaeoecology. As previously stated, the lithology of the Burnside Mudstone is homogeneous and fine-grained, having a median diameter of 0·006 mm. and a Trask sorting coefficient of 2·23. In fresh outcrop the mudstone is massive, having no sedimentary structures except filled borings. Though not abundant, the macrofossils include several thin-shelled mollusca as *Ctenamussium sp.*, *Ostrea sp. nov.*, *Lima* (*Callolima*) *sp.* cf. *L. regia* Suter (Marwick 1939, p. 59), together with thin-shelled indeterminate terebratulids, small echinoid spines, and sponge spicules. Chapman (1934, p. 119) has described a teleostean fish, *Eothyrsites holosquamatus*, from the Burnside Quarry, and fish scales are relatively common.

The sediment and macrofossils indicate continuous sedimentation in quiet waters. Many of the bivalves have both valves attached and the fossils are distributed throughout the mudstone. Of the foraminifera Mr. N. de B. Hornibrook, Senior Micropalaeontologist, N.Z. Geological Survey, writes (personal communication dated 13 January 1958): 'The Burnside Mudstone contains a very rich foraminiferal fauna characterized especially by a large and varied assemblage of Lagenidae. Polymorphinidae (several species of *Guttulina*, *Globulina*, and *Pyrulina*) are also common and large. The Heterohelicidae are represented only by large well-developed *Plectofrondicularia whaingaroica* (Stache) but Buliminidae are well represented and include abundant large *Bulimina* and *Uvigerina*. Anomalinidae include abundant *Cibicides* and *Anomalinoides*. *Pullenia*, *Sphaeroidina*, and *Gyroidinoides* are abundant and so are the pelagic forms *Globigerina linaperta* Finlay and *Globigerinoides index* Finlay.

'The almost complete absence of Miliolidae and Elphidiidae and other shallow-water forms makes it very unlikely that the Burnside Mudstone was deposited in shallow water.

'By analogy with Recent faunas, and especially because of the abundant Lagenidae and pelagic species, a fairly deep-water environment (of the order of 100 fathoms), such as that provided by the outer continental shelf, seems most likely.'

Such an environment corresponds closely with the present-day habitats of Veretillids, which, as Kolliker (1880, p. 31) notes, are the only group of Pennatulids found at such shallow depths, whilst 'all the others are, with very few exceptions, deep-sea forms'. Undisturbed conditions are necessary for the preservation of Pennatulids but in the case of *Bensonularia spatulata* this may have been aided by the presence of muscle fibres in the epidermis of the coenenchyme (Hyman 1940, p. 545). Probably these muscles were well developed in *Bensonularia spatulata* in order to support the relatively large rachis.

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LOWER TOURNAISIAN TRILOBITES IN THE CARBONIFEROUS LIMESTONE FACIES OF THE SOUTH-WEST PROVINCE OF GREAT BRITAIN AND OF BELGIUM

by ROLAND GOLDRING

Abstract. Trilobites from the lowermost beds of the Carboniferous, from the south-west Province and from Belgium are described. The species are assigned to *Moschoglossis* gen. nov., *Cummingella?*, *Piltonia*, and *Brachymetopus*. The trilobite fauna is regarded as a limestone facies fauna of the *Gattendorfia* Stage.

INTRODUCTION AND STRATIGRAPHY

As a continuation to the author's (1955) description of the Upper Devonian and Lower Carboniferous trilobites of the Pilton Beds (sandstone-shale facies) in north Devon, south-west England, the trilobites of the lowest beds of the Carboniferous Limestone have been investigated. The present material has been assembled from museums in Great Britain, from the Musée royal d'Histoire naturelle in Brussels, and by collecting from the Lower Limestone Shale (Kellaway and Welch 1955, p. 8; K Zone of Vaughan 1905, p. 189) in the Avon Gorge, Bristol.

Trilobites are uncommon in the lowest Carboniferous Limestone but specimens of *Moschoglossis*, *Piltonia*, and *Brachymetopus* were found in the Lower Limestone Shale of the Avon Gorge. *Phillipsia truncatula* auct., which is not described in the present paper, occurs relatively more commonly than the above genera in the upper part of the Shale, towards the top of K_2, and in β. Collecting at Portishead, near Bristol, in the Mendips, and in Pembrokeshire yielded only *Phillipsia truncatula* auct., although specimens of *Moschoglossis* have been identified in museum collections from Portishead. The author has not collected in Belgium.

In the south-west Province of the Carboniferous Limestone in Great Britain the highest beds of the Upper Old Red Sandstone are conformably overlain by the Lower Limestone Shale. The Shale varies in thickness from over 500 feet in the Mendips to about 200 feet in the Avon Gorge, and from 300 to 600 feet in Pembrokeshire.

In Belgium (Delépine 1940) the marine Upper Devonian, Comblain-au-Pont Beds, equivalent to the Étroeungt Beds of north France, are succeeded by the Hastière Limestone (Tn1b). This is in turn followed by the Shales with *Spiriferellina peracuta* (Tn2a) and the Landelies Limestone (Tn2b); the highest horizon covered by the present study.

None of the species here described has been previously described from the cephalopod facies, in Germany or England, or from the Pilton Beds. The ranges of the species and genera in the relevant areas are as follows:

Moschoglossis. In Britain *M. decorata* is found at the base of K_2 and ranges at least into Z, Black Rock Limestone. In Belgium it is found in Tn1b, and ranges into Tn2b and possibly higher. No species of the genus has yet been recorded from the Pilton Beds of Devon. Nor can the genus be recognized in the large trilobite faunas described from

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the U.S.S.R. (Weber 1937), though Weber (1937, p. 145) mentions the presence of pygidia which may belong to the genus.

Cummingella is doubtfully present in the Lower Limestone Shale.

Cyrtosymbole. No species of *Cyrtosymbole* have been found in the lowest Tournaisian facies of Britain or Belgium in contrast to the prominence of species of *C.* (*Macrobole*) and *C.* (*Waribole*) in the cephalopod facies and in the Pilton Beds. *C.* (*Waribole*) *sargaensis* (Weber 1937, pl. 1, 2) from the Urals is close to *C.* (*Waribole*) *abruptirhachis* (R. and E. Richter 1919; 1951, pl. 1) from Germany.

Liobolina. This genus is only known from the cephalopod facies of Germany, where it is confined to the *Gattendorfia* Stage.

Piltonia. Piltonia fryi appears in the Avon Gorge, Bristol near the base of K_1 and ranges probably into β. In Belgium it is doubtfully present below the Hastière Limestone but definitely occurs in the Hastière Limestone, *peracuta*-Shales, and Landelies Limestone. *P. kassini* occurs in the Kassin Beds of the Kirghiz Steppe, and possibly in the southern Urals (Balaschova 1956), and *P. salteri* in Pilton Beds C. *Piltonia* may be regarded as a genus typical of the lowest Tournaisian.

Brachymetopus. Only a fragment of *Brachymetopus* is known from the Carboniferous Limestone of south-west England, and it is poorly represented in Germany. In contrast it is common in the Pilton Beds.

Phillipsia has not been recorded below the top of K_2 in Britain and below Tn2b in Belgium. The record of *P. gemmulifera* from Tn2a (Paul 1937*b*, p. 13) has not been substantiated. It is highly unlikely that this species is present at so low a horizon and the record may refer to *Piltonia fryi.*

The correlation of the Lower Limestone Shale with the Pilton Beds and with their equivalents on the continent of Europe is a difficult problem. Paul (1937*a*, p. 435) concluded, mainly on brachiopod evidence, that the upper part of the Shale (K_1 and K_2) is equivalent to the Hastière Limestone, and in a more comprehensive paper he (1937*b*, table 1) correlated the Hastière Limestone and *peracuta*-Shales with the Hangenberg Limestone of Germany (*Gattendorfia* Stage). The base of the Tournaisian is here taken as the base of the *Gattendorfia* Stage and not at the base of Tn1a, Comblain-au-Pont Beds, of Belgian nomenclature, or T_1 of Paul (1937*b*), although the Belgian coding is retained in describing the location of specimens.

As George has remarked (1952, p. 35) it is not possible to apply the ammonoid chronology to the lowest beds of the Carboniferous Limestone. The presence of *Gattendorfia*, associated with trilobites typical of the *Gattendorfia* Stage, in Pilton Beds B affords good correlation of this part of the Pilton Beds with the *Gattendorfia* Stage. R. and E. Richter (1951, p. 229) proposed three parachronological Stages (Stufen) for the Lower Carboniferous; the *Liobolina*, *Liobole*, and *Phillibole* Stages, equivalent respectively to the *Gattendorfia*, *Pericyclus*, and *Goniatites* Stages of the orthochronology. The genus *Moschoglossis* has morphological similarities with *Liobolina*, and its presence in the Lower Limestone Shale of the Bristol area and in the Lower Tournaisian of Belgium accompanied by *Piltonia* is therefore interesting for the stratigraphical correlation of the Lower Tournaisian with the cephalopod succession as developed in Germany and with the Pilton Beds of north Devon.

Whilst it is not proposed to enter into a critical correlation of the British and Belgian areas it would seem that there is no evidence that K_1 and K_2 are not lowermost Carboniferous, and it is suggested that the Hastière Limestone (Tn1b) and the *peracuta*-Shales (Tn2a) may together be equivalent to the Lower Limestone Shale (K_1 and K_2) rather than to β as suggested by Vaughan (1915). This is a slight emendation of the correlation proposed by Paul (1937*a*). The base of the Black Rock Limestone may be then nearly equivalent to the base of the Landelies Limestone (Tn2b). The Lower Limestone Shale (K_1 and K_2) may be correlated with at least part of the *Gattendorfia* Stage.

The trilobite fauna of the lowest Tournaisian in Belgium and south-west England is not typically Tournaisian or Dinantian. *Phillipsia* is for the most part absent and *Cummingella* questionably present. *Weberides* and *Griffithides* are both absent. Moreover, the fauna has no Famennian aspect as there is no sign of *Phacops*. It is, however, a distinct fauna, with elements which compare with the trilobite fauna of the *Gattendorfia* Stage in Germany and north Devon. It may therefore be regarded as a limestone facies trilobite fauna as opposed to that typical of the cephalopod facies of the *Gattendorfia* Stage.

Preservation of material. Whilst collecting in the Lower Limestone Shale of the Bristol area I noticed that trilobites were to be found in only one type of lithology. In other types they were extremely uncommon. The thin limestone bands in which they occur are rubbly-weathering and have a most conspicuous lack of preferred orientation of the contained fossils. The fossils are for the most part well separated from each other and well preserved, and show no signs of abrasion, though the pygidia and cranidia were always separate. Examination by microscope indicated many shells and limestone fragments. In the thin limestone bands small (5 mm.) Athyrids were very abundant; '*Avonia*' *bassa* and species of *Chonetes* and *Schellwienella* were quite common, but crinoid ossicles notably rare. In other limestones showing a bedded arrangement of the fossils, and in particular in '*Chonetes*-sands', the trilobites were very rare or absent. The shales were not exhaustively searched because of the poor preservation of fossils in them. Collecting elsewhere, in the Mendips and in Pembrokeshire, yielded no bands with randomly orientated shells and no trilobites were found.

The assembled material from British museums supports the conclusion that there is a greater abundance of trilobites in the one type of lithology. All the Portishead trilobites are in this type of limestone, though with these crinoid ossicles are common. Several other specimens are in a crinoid sand. The Belgian trilobites occur in more varied lithologies. Those from the Landelies Limestone (Tn2b) are mostly in 'petit-granit', but those from the Hastière Limestone (Tn1b) do lack a preferred orientation.

Bohlin (1949, p. 558) has described limestones with similar random orientation of the fossils from the Ordovician of Öland, Sweden and has discussed their origin. It is likely that this type of limestone occurs not uncommonly elsewhere.

Terminology. The terminology used in description is that of Goldring (1957). In description the side and front views essentially refer to the profiles seen in these aspects, whereas the plan is a description in general. In the side and front views of cranidia, the plane perpendicular to the median plane (sag.) of the glabella and occipital ring and touching them is placed horizontally. Although this seldom corresponds with the horizontal plane of the cephalon in life, the orientation allows for a more definite description, is more easily appreciated, and can be more accurately reproduced, in these particular species (cf. R. and E. Richter 1956, p. 367; orientation of cephalon in side view).

Material. Described and figured specimens are deposited in museums, abbreviated in description as follows: BC—Bristol City Museum, England. BM—British Museum (Natural History), London. BR—Musée royal d'Histoire naturelle, Brussels. BU—Bristol University (Department of Geology), England. GS—Geological Survey Museum, London. HM—Hunterian Museum, Glasgow, Scotland. O—University Museum, Oxford, England. SMF—Senckenberg Museum, Frankfurt am Main, Germany.

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DESCRIPTIONS

Genus MOSCHOGLOSSIS gen. nov.

Derivation of name. Greek—calf's tongue—from the shape of the glabella.
Type species. Moschoglossis decorata decorata subsp. nov.
Range. Lower Carboniferous, Tournaisian.
Distribution. England, Bristol area, Lower Limestone Shale; Belgium, Dinant synclinorium; France, Avesnelles; ?U.S.S.R., Urals.
Species assigned to the genus. The type species comprising *M. decorata decorata* and *M. decorata brevicauda* subsp. nov.

Diagnosis. Glabella cylindrical and moderately inflated. Occipital ring an even band, scarcely narrower at the axial furrows than medianly. No branch furrow. Large eyes and narrow palpebral lobes. High narrow anterior border. Anterior branch of facial suture rather strongly diverging and β strongly rounded. Anterior fixed cheek markedly triangular. γ opposite glabellar furrow 3p and close to axial furrow. ϵ slightly posterior to half length of glabellar lobe 1p. Posterior branch strongly diverging. Free cheeks with small genal spine. Pygidium with thirteen rings and nine ribs. Weak or absent border furrow. Ring and pleural furrows weak, and anterior and posterior portions of ribs equally developed. Ornament on glabella of fine transverse scale-like ridges with steep posterior edges: much finer on occipital ring and pygidium.

Material. Cranidia, free cheeks, pygidia, and hypostome.

Comparisons with other genera. 1. *Cummingella* Reed 1942. The type species of *Cummingella*, *C. jonesi* (Portlock 1843) (Opinion 352. Opinion and Declaration rendered I.C.Z.N. vol. **11,** pt. 2, pp. 25–46, 1 pl., 1955) is closely comparable with *M. decorata* only in some details. The glabella of the two species differs considerably, that of *C. jonesi* being anteriorly inflated so that the breadth anteriorly is as great as the breadth posteriorly. In other species assigned to *Cummingella* the anterior part is still more inflated and the breadth anteriorly is the greatest breadth. In *C. jonesi* the facial suture closely follows the axial furrows and the anterior part of the fixed cheek is extremely narrow, whereas in *M. decorata* β is sharper, γ–β diverges more strongly from the median line, and the anterior fixed cheek is comparatively large. The steep anterior border in *C.*

jonesi is close to that in *M. decorata* but in *C. jonesi* carries down posteriorly below the glabella, whereas in *M. decorata* the border continues the line of the glabella, though offset. The size of the large eyes is very similar, though the Russian variety *C.* '*derbyensis* var. *kargini*' (Weber 1933) has comparatively small eyes. The lateral terminations of the occipital ring in *C. jonesi* are similar to those in *M. decorata*, and the form of the posterior border of the fixed cheek is also similar in both. The glabellar furrows are more strongly incised in *jonesi*, where 1p reach to the occipital furrow. The free cheeks of the two species are very similar, and short genal spines are present in both.

The pygidia of *C. jonesi* and *M. decorata* differ in that *C. jonesi* has more prominent rings and ribs, and deeper ring and pleural furrows, though each has the same number. The posterior portions of the ribs in *C. jonesi* are comparatively narrower than in *M. decorata*. Both species have broad borders.

The main difference between *M. decorata* and *C. jonesi* is in the shape of the glabella. The anterior inflation of the glabella with geological time is a well-known trend in trilobites, and the several points of close similarity between *C. jonesi* and *M. decorata* suggests that *Moschoglossis* may be a forerunner of *Cummingella*.

2. *Liobolina* R. and E. Richter 1951. Type species *L. nebulosa* R. and E. Richter 1951. The outline of the glabella in *M. decorata* is similar to that in *Liobolina*. Apart from this the cephalon of *M. decorata* differs in detail from the cephalon of the two species included in *Liobolina*, *nebulosa* R. and E. Richter 1951, and *submonstrans* R. and E. Richter 1951. The anterior border of the cranidium in *M. decorata* is much steeper than in either *L. nebulosa* or *L. submonstrans*. The occipital ring also differs in that laterally it only slightly shortens and is almost as long at the axial furrows as it is centrally (sag.). Of the two species the free cheek is only known in *L. nebulosa* and the genal angle is strongly rounded. The course of the facial suture and the size of the eyes are very different in *M. decorata* from those in *L. nebulosa* and *L. submonstrans*. In *L. nebulosa* the palpebral lobe is practically absent and the posterior branch of the facial suture diverges from the axial furrow. In *L. submonstrans* the palpebral lobe is small, more or less centrally placed to the glabella (glabellar furrow 1p slightly anterior to ϵ), and the posterior branch of the facial suture is rather long and for nearly half its course parallels the axial furrow. In *M. decorata decorata* the palpebral lobe is large and extends almost to the occipital furrow. ϵ is situated far posterior and a part of the posterior branch of the suture which parallels the axial furrow is virtually absent. ϵ and, especially, γ are also rather closer to the axial furrow than in *L. submonstrans*. In *L. nebulosa* they are well away from the axial furrow. The glabellar furrows are weak in all three species, but the slight anterior fork in furrow 1p in *M. decorata* is not discernible in either *L. nebulosa* or *L. submonstrans*.

The pygidium of *M. decorata* is similar to the pygidium of *L. nebulosa* and *L. submonstrans* in that the segmentation is weak, though it is less so in *M. decorata*. The position of the rib furrow is similar in all species. *M. decorata* has a greater number of axial rings, thirteen as against nine plus two more indistinct rings in *L. submonstrans* and *L. nebulosa*, and probably also a greater number of ribs, nine as against six plus considerable room for more in *L. submonstrans* and *L. nebulosa*.

The size of the eyes may well be due to an environmental factor; the large eyes associated with the species from the Carboniferous Limestone facies and the small or absent eyes from the cephalopod facies. Blindness in trilobites from the Upper Devonian and

Lower Carboniferous has been discussed by R. and E. Richter (1951, p. 226). It is particularly prominent amongst Upper Devonian and Lower Carboniferous species from the cephalopod facies.

Although *M. decorata* has some resemblances to *L. nebulosa* and *L. submonstrans*, the similarity is not sufficiently close for it to be considered a species of *Liobolina* in the Carboniferous Limestone facies. The several points besides the facial suture on which it differs from *L. nebulosa* and *L. submonstrans* are considered to be sufficiently distinct for it to be assigned to a new genus.

Moschoglossis decorata decorata subsp. nov.

Plate 43, figs. 1–7

Derivation of name. Manuscript name given by F. R. C. Reed to pygidium (HM A 495) which, characteristic of the species, has scale-like ornamentation.
Holotype. Cranidium (GS 86982), Pl. 43, fig. 1.
Type locality. Bristol, Avon Gorge, right bank, from scree at end of wall, by bed marked '*Chonetes* cf. *buchiana*' on pl. 2 of Vaughan 1906.
Horizon. Carboniferous Limestone, Lower Limestone Shale, K_2 Subzone (Vaughan 1905).
Material. A few cranidia, together with free cheeks and pygidia probably belonging to the species.

Diagnosis. Cranidium and free cheek: as for genus. Pygidium with length rather greater than breadth of axis plus 1 pleural lobe. No border furrow.

Description. Cranidium, side view. Glabella anteriorly moderately curved. Posterior $\frac{1}{3}$ and occipital ring almost flat, the occipital ring continuing the line of the glabella. Occipital furrow sharp. Very short (sag.) but high anterior border, which almost parallels the offset line of the glabella.

Front view. Glabella a triplet of three very low arches, which together form a low curve. The outer two are narrower than the central one and steepen towards the axial furrow, which is rounded. Palpebral lobes narrow and weakly arched.

Plan. Anterior margin only moderately curved. Border very narrow and with eight to ten parallel lines. Glabella almost rectangular, with a slight nick scarcely constricting the glabella between glabellar furrows 2p and 3p at about half length of glabella, anterior to which it is almost parallel-sided with a broad, rounded termination. Posteriorly it broadens slightly and is broadest at glabellar furrows 1p but there only slightly broader than the anterior part of the glabella. Posterior to furrows 1p it narrows very

EXPLANATION OF PLATE 43

Figs. 1–7. *Moschoglossis decorata decorata* subsp. nov. 1–3, plan, front view, and side view of holotype cranidium, ×3, (GS 86982); 4, free cheek, ×3 (GS 95324); 5–7, plan, side view, and posterior view of pygidium, ×2·5 (BM I 13569).

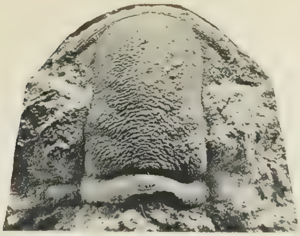
Figs. 8–11. *Moschoglossis decorata brevicauda* subsp. nov. 8, 9, plan and side view of holotype pygidium, ×5 (BR IG 13829/1); 10, 11, plan and side view of hypostome, ×5 (BR IG 13828).

Fig. 12. *Moschoglossis sp*. A, cranidium, ×4 (GS 33713).

Fig. 13. *Cummingella? sp*., cranidium, ×3 (GS 95325).

Figs. 14–16. *Cummingella? costabisulca* sp. nov., plan, side view, and posterior view of holotype pygidium, ×4 (GS 33712).

Figs. 17–20. *Piltonia fryi* sp. nov. 17–19, plan, side view, and posterior view of holotype pygidium, ×3 (GS 86984); and 20, pygidium, ×5 (BR IG 9136).



1
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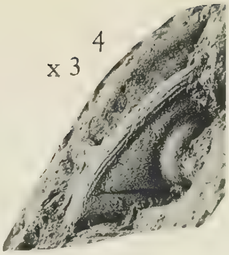

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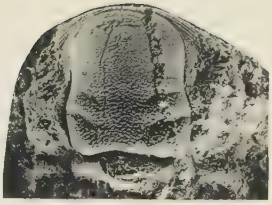

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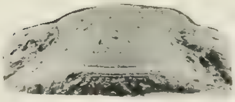

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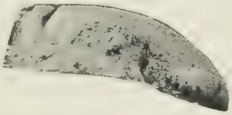

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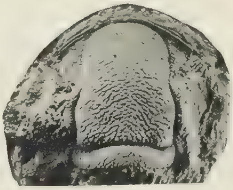

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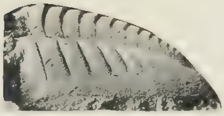

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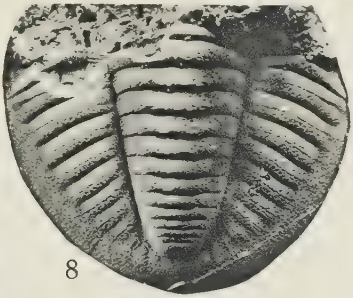

8
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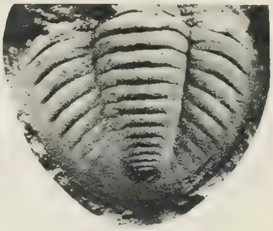
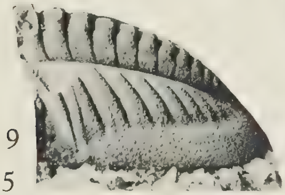


5
x 2.5



9
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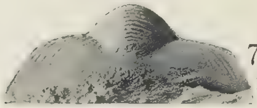
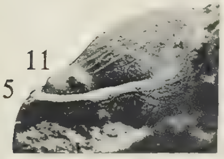


7
x 2.5



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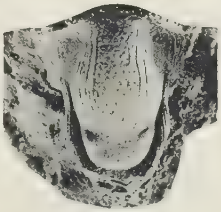
x 5



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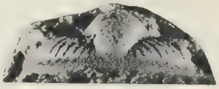
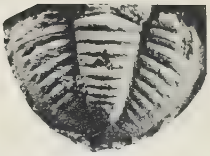
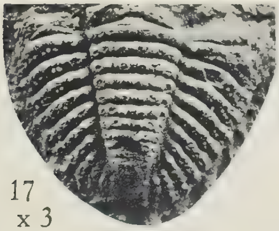


16
x 4



14
x 4



17
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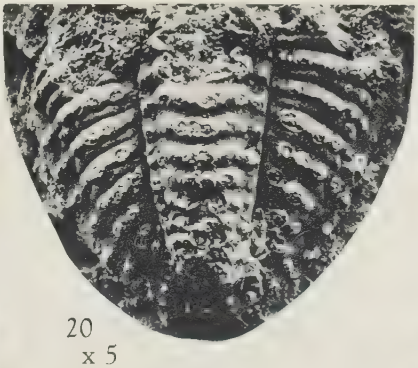

20
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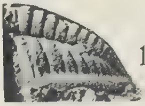
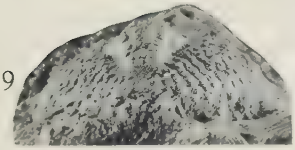


15
x 4



19
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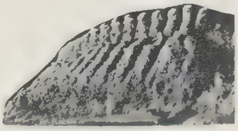

18
x 3

GOLDRING, Lower Tournaisian trilobites

slightly to the occipital furrow. Four pairs of glabellar furrows which are not impressed; they are scarcely discernible, and almost only so because they lack ornamentation. 1p strongly rounded, clear at the axial furrows, and forking with very short anterior branch furrow. Posterior branch not quite reaching to the occipital furrow; the distance between the posterior terminations of the furrows rather less than half the maximum breadth of the glabella. 2p almost straight. 3p and 4p parallel to 2p; 4p only a slight mark. Occipital furrow arches slightly anteriorly, medianly, and towards the axial furrows. The occipital ring is scarcely narrower at the axial furrows than medianly and bears a small occipital node.

Facial suture. Anterior branch moderately diverging from the glabella. β strongly rounded and rather angular; anterior fixed cheeks triangular. γ close to the axial furrow and opposite glabellar furrows 3p. ϵ slightly posterior to half length of glabellar lobe 1p. Palpebral lobe long and narrow, widest about opposite to glabellar furrows 1p. β only just farther from the median line than δ. Posterior branch almost immediately running outwards, terminating at a distance from the axial furrow about equal to one-third breadth (tr.) of occipital ring, though in the cranidium (GS 63063) the right termination is at a distance equal to half the length of the occipital ring. Posterior border furrow scarcely discernible and posterior border very narrow, only one-third length of occipital ring. Posterior fixed cheek very narrow.

Ornamentation. Glabella and occipital ring with fine transverse scale-like ridges with steep posterior edges. The ridges are much finer on the occipital ring. Towards the anterior margin and on the anterior fixed cheek the ridges become weaker and are accompanied by a fine punctation. The palpebral lobes are finely punctate.

Free cheek. Rather longer than broad. Cheek area evenly but not strongly arched, and with slight levelling around the eye. Eye large and regularly curved. Lateral border furrow indistinct and lateral border, like anterior border of cranidium, strongly rounded and with eight to ten parallel lines. Posterior border furrow rather sharp and V-shaped; the posterior border weakly arched but moderately wide. A short blunt genal spine.

Pygidium. Side view. Axis rather less high than pleural lobe, curving gently and evenly and terminating a little sharper at the border. Only a slight re-entrant angle between the axis and the border, which has the same convexity as the axis. The rings are scarcely arched but all are distinct and scale-like with sharp posterior edges.

Rear view. Axis rather strongly curved. Pleural lobes flat near the axial furrows, then arching strongly and falling steeply to the margin.

Plan. Length rather greater than breadth of axis plus one pleural lobe. The axis tapers gently with almost straight sides to a broad rounded termination which is not succeeded by any post-axial ridge. The border is wide and is not separated from the ribs by any furrow.

Thirteen rings, all distinct. Ring furrows sharp, abruptly constricting to only a fine line between trace of longitudinal grooves and axial furrows. Longitudinal grooves generally not discernible and otherwise extremely weak (GS 63062). Ring 1 slightly shorter than 2. 1–4 slightly arched anteriorly.

Ribs 1–4 distinct, 5–7 less distinct, and 8 and 9 indistinct. The ribs are moderately curved but scarcely arched, and the pleural furrows narrow and sharp. Rib furrows, which divide the ribs into equal parts, only a trace but distinct on ribs 1–5, and on rib 1 pass on to the border. The ribs do not continue on to the border.

Ornamentation. At ×20 punctate, and with fine short scale-like ridges, much weaker than on the glabella but similar to those on the occipital ring. Near to the margin laterally are numerous fine lines which approach the margin posteriorly and meet it at an acute angle.

Measurements (in mm.)

	GS 86982 Pl. 43, fig. 1	GS 63063
Length of cranidium	9·1	8·5
Length of glabella	7·1	6·7
Breadth of glabella	5·1	4·8

	BM I 13569 Pl. 43, fig. 5	GS 63062	BU 1146/2	BU 1147/1
Length of pygidium	9·6	10·4	8·0	4·8
Breadth of pygidium	11·0	13·8	. .	6·0
Length of axis	8·1	9·0	6·7	4·1
Breadth of axis	4·5	5·1	4·0	2·5

Comparisons. For comparisons with *Cummingella jonesi* Portlock 1843, *Liobolina nebulosa* R. and E. Richter 1951, and *L. submonstrans* R. and E. Richter 1951 see pp. 234–6. Weber (1937, p. 145) stated that in the Lower Tournaisian of the Urals pygidia similar to *Cummingella* '*derbyensis* var. *kiritchenkoi*' (Weber 1937) are present, but he did not say how the variety differed and gave no figures.

Occurrence. England, Lower Limestone Shale. Holotype (above) and pygidia (GS 86983); Bristol, Avon Gorge, indefinite locality but accompanied by '*Avonia*' *bassa* (Vaughan), with lithology resembling that of holotype, cranidium, free cheek, pygidium (GS 63062–4); Avon Gorge, indefinite locality but probably Lower Limestone Shale, with *Camarotoechia mitcheldeanensis* Vaughan and *Chonetes* cf. *hardrensis* (Phillips), cranidium, pygidium, and free cheeks (GS 95324, ? 95326, 95327); Bristol, Westbury-on-Trym, St. Monica's Home (Reynolds and Smith 1925, p. 469), free cheek and pygidia (BU 1146/1–3, 1147/1–2), Coombe Farm, Cherry Orchard (562.777), pygidium (O E1365); a single pygidium from the Avon Gorge (BU 1149) is labelled Z Zone (the presence of the species in Z has not been confirmed by present collecting); Portishead, near Bristol, indefinite locality but almost certainly Nightingale Valley Quarry (450.752), pygidia (BM I13569, HM A495, O E1352–3).

Moschoglossis decorata brevicauda subsp. nov.

Plate 43, figs. 8–11

Derivation of name. From the comparatively short pygidium.
Holotype. Pygidium (BR IG 13829/1), Pl. 43, fig. 8.
Type locality. Feluy 41, Feluy, abandoned quarry east of Feluy 31.
Horizon. Carboniferous Limestone, Tournaisian, Landelies Limestone (Tn2b).
Material. Pygidia, together with cranidium, hypostome, and free cheeks probably belonging to the species.

Diagnosis. A subspecies of *M. decorata* with the following differences from *decorata decorata*: pygidium comparatively shorter and length only very slightly greater than the breadth of axis plus one pleural lobe. Slight border furrow.

Description. Cranidium. The only incomplete cranidium (BR IG 13829/2), showing part of the glabella and anterior border, does not differ in form or ornamentation from *M. decorata decorata.*

Hypostome (BR IG 13828—posterior border broken). Anterior margin weakly curving posteriorly to the anterior wings. Anterior wings moderately projecting with almost straight outer margins, strongly curving inwards and upwards to lateral margins. Lateral margins subparallel, diverging slightly to weak shoulders and then converging more sharply to the broken, but apparently rather narrow, rounded termination. Middle body strongly convex transversely, not separated or defined anteriorly from wings, but laterally outlined by sharp furrow and posteriorly by sharp change of slope. Longitudinally it is moderately and evenly convex to four-fifths length. Posterior fifth separated by gradual concave slope, then dropping with subgeniculate bend to border. Two small lateral prominences (maculae) just posterior to change in slope. Posterior border flat, becoming convex towards wings. Strong lines present on all surfaces except on crest of middle body, between middle body and wings, and on border posterior to shoulders.

Free cheek. The several free cheeks show no differences in form or ornamentation from *L. decorata decorata.*

Pygidium. Side view. In comparison with *M. decorata decorata* the axis in side view falls more steeply posteriorly and there is a distinct and sharp drop at the termination.

The posterior view does not differ in any respect.

In plan the proportions differ from those of *M. decorata decorata.* The pygidium is comparatively shorter and the length is only very slightly greater than the breadth of the axis plus one pleural lobe. The number and prominence of the rings and ribs is the same and the incision of the ring, rib, and pleural furrows agrees in all respects. A slight but distinct border furrow is present at the termination of the rib and pleural furrows, and very weak longitudinal grooves may be present. The ornament agrees with that of the previous species.

Measurements (in mm.)

	BR IG 13828	BR IG 13829/1 Pl. 43, fig. 8
Length of pygidium	6·3	7·5
Breadth of pygidium	7·8	9·0
Length of axis	5·4	6·2
Breadth of axis	3·3	3·6

Remarks. The subspecies is incompletely known, morphologically and stratigraphically. Although the main known differences with the nominate-subspecies are of shape and not ornamentation, it would seem preferable to use ternary nomenclature rather than to erect a new species.

Occurrence. Belgium (all specimens in BR); Hastière Limestone (Tn1b), Methel 4, Ermeton s/Biert, railway cutting, pygidium (IG 13.777); *peracuta*-Shales (Tn2a) Landelies, quarry, pygidia (IG 10024, IG 10004); Landelies Limestone (Tn2b), Feluy, old quarry east of Feluy 31, holotype pygidium, free cheek (IG 13.829), Feluy, canal de Charleroi, lock 30, hypostome, pygidium (IG 13.828), Feluy, Rocque quarry, level 6, free cheek (IG 13827); Hastière, Meuse Valley between Km. 100.3 and 100.4, pygidium (IG 10234); France, Avesnelles Shales, Avesnelles, pygidia (SMF 3798).

Moschoglossis sp. A

Plate 43, fig. 12

A single cranidium (GS 33713) from the Avon Gorge, Bristol, but without precise locality, and without other stratigraphically indicative species on specimen, differs from *M. decorata* sp. nov. in the following points:

The anterior border is proportionally slightly longer (sag.) and the glabella broadens more sharply to the maximum breadth at glabellar furrows 1p.

The specimen differs sufficiently from the previous species to be considered as a separate species and the differences are not considered to be merely due to the immaturity of the specimen. Specimens of *Liobolina nebulosa* R. and E. Richter 1951 with similar variation in size have been examined and the smaller of these show no such differences from the larger and type specimen.

Measurements in mm.: length of cranidium 5·0, length of glabella 4·0, breadth of glabella 3·0.

Genus CUMMINGELLA Reed 1943

Cummingella? costabisulca sp. nov.

Plate 43, figs. 14–16

Derivation of name. From the cloven ribs.
Holotype. Pygidium (GS 33712), Pl. 43, fig. 14.
Type locality. Bristol, Avon Gorge, without precise locality.
Horizon. Carboniferous Limestone, possibly Lower Limestone Shale.
Material. Only pygidia known.

Diagnosis. A species possibly of *Cummingella* with the following characteristics: pygidium strongly rounded with length about equal to breadth of axis plus one pleural lobe. Broad smooth border. Twelve rings and eight (+one) ribs. Sharp rib furrows, more prominent at border furrow, dividing ribs into equal portions.

Description. Pygidium. Side view. Axis somewhat less high than pleural lobes, sloping with only slight curvature to ring 7, then more steeply to last ring. Axis terminates steeply and rather sharply to border, which is broad but only weakly arched. Rings all clearly outlined, the first moderately arched, the remainder weakly arched but with sharp posterior edges.

Posterior view. Axis strongly arched. Inner parts of pleural lobes almost flat, curving over strongly to flat outer parts of lobes.

Plan. Length of pygidium approximately equal to breadth of axis plus one pleural lobe. Axis only slightly narrower than a pleural lobe, tapering rather strongly with almost uncurved sides and ending in a broad blunt termination. No postaxial ridge but termination of axis not clearly bounded. Border broad (rather more so posteriorly than in fig. 14) and weakly convex, separated from the ribs by a broad border furrow which makes a distinct re-entrant between the ribs and border.

Twelve distinct rings. Ring furrows rather sharp and narrow, constricting sharply before axial furrows but continuing to them. Anterior edge of ring 1 arches forwards medianly; remainder even bands.

Eight (+one) ribs. Ribs 1–5 gently curved; the remainder almost straight. Pleural furrows sharp and incised. Rib furrows, which divide ribs into almost equal parts, weak but distinct on ribs 1–6, becoming more prominent towards the border furrow, where they are like a deep elongated pit cleaving the ribs. Both portions of ribs weakly arched, the anterior portions rather greater. The anterior portions narrow slightly laterally and especially near the border furrow, where the anterior portions of the ribs are rather higher than the posterior portions. The posterior portions widen slightly laterally. Both portions of ribs continue shortly on to the border; the anterior portions slightly farther. Outer two-thirds of border non-undulating.

Ornament. At ×20 both ribs and rings with fine granulations. The border antero-laterally bears numerous fine lines approaching the margin posteriorly.

Measurements (in mm.)

	GS 33712 Pl. 43, fig. 14	BC Cb 3756
Length of pygidium . . .	4·3	4·5
Breadth of pygidium . . .	5·5	(5·5)
Length of axis	3·5	(3·5)
Breadth of axis	2·0	(2·0)

Comparisons. The species differs from '*Griffithides?*' *carringtonensis* Woodward (1884, p. 41, pl. 9 figs. 6*a*–*b*; refigured in Weber, 1937, pl. 11, fig. 17) in having a narrower axis and more strongly curved ribs. It differs from *Phillipsia laticaudata* var. *kuzneciana* Weber (1937, pp. 6, 127, pl. 5, figs. 21–23) from U. Tournaisian and L. Visean in having the rib furrow more centrally placed.

Remarks. The species is assigned tentatively to *Cummingella* because of the broad border, well-defined border furrow, and prominence of the rib furrows about where they meet the border furrow.

Occurrence. Carboniferous Limestone, probably Lower Limestone Shale, Bristol, England. Holotype, above; (BC Cb 3756) as for holotype—this specimen has the label 'Bristol, Cook's Folly, Sneyd Park'. Cook's Folly occupies ground stratigraphically lower than the Bryozoa Bed (Km.) which outcrops along the south boundary of the property. The specimen therefore did not come *in situ* from this locality. Cook's Folly is a locality which was commonly given at the beginning of the century to specimens collected from the right bank of the Avon in K_1, K_2, β, and the lower part of Z.

Cummingella? sp.

Plate 43, fig. 13

A single cranidium (GS 95325) from the Avon Gorge, Bristol, but without precise locality, and without other stratigraphically indicative species on specimen, differs from *M. decorata* sp. nov. in the following points:

Although the cranidium is broken longitudinally by a calcite vein, the glabella is comparatively shorter. The anterior branch of the facial suture only weakly diverges from the glabella and the anterior part of the fixed cheek is narrow. δ is farther from the median line than β. The ornamentation is of granules which have steep posterior edges rather than ridges.

Measurements in mm.: length of cranidium 8·2, length of glabella 6·5, breadth of glabella (5·0).

Genus PILTONIA Goldring 1955

Piltonia fryi sp. nov.

Plate 43, figs. 17–20

Derivation of name. After Mr. T. R. Fry of Bristol.
Holotype. Pygidium (GS 86984), Pl. 43, fig. 17.
Type locality. Bristol, Avon Gorge, right bank, from weathered rock at end of wall, by bed marked '*Chonetes* cf. *buchiana*' at end of wall in pl. 2 of Vaughan 1906.
Horizon. Carboniferous Limestone, Lower Limestone Shale.
Material. Pygidium and incompletely known cranidium and thorax.

Diagnosis. A species of *Piltonia* with the following characteristics: Longitudinally elliptical. Breadth of axis slightly greater than breadth of a pleural lobe. Twelve tubercular rings. Ten tubercular ribs; two posterior to axis. Anterior portions of ribs more strongly developed than posterior portions.

Description. Cranidium and thorax. (*a*) A compressed, partially preserved specimen (BR IG 10865) has a cylindrical glabella with only slight constriction at about one-half length. It bears coarse tubercles. Glabellar lobes 1p prominently demarcated by strong furrows which join the occipital furrow at two-sevenths breadth of glabella. Glabellar furrows 2p and 3p sharp. Anterior fixed cheek with tubercles. Only anterior part of facial suture discernible and moderately diverging. Anterior border not clear but distance from anterior end of glabella to margin very short. Thorax with tubercular segments.

(*b*) Two fragmentary cranidia (BU 1144, 1148) may belong to the species. No pygidia have been found with them at the locality, which is at a higher horizon than that at which any other pygidia have been found. Both cranidia show a coarsely tubercular glabella and one shows a distinct subcranial furrow. This distinguishes them from species of *Phillipsia*, which occur commonly at the locality, and is the sole criterion for assigning them to the species.

Pygidium. Side view. Axis less high than pleural lobes, curving gently to last ring, and then falling steeply to long, and only slightly convex, postaxial portion. Rings prominent, strongly arched, and with steep posterior slopes. They bear tubercles and the furrows are deep and rounded. Ring 1, postannulus, is much higher than ring 2.

Posterior view. Outline of ring 1, postannulus, almost trapezoidal with nearly flat sides and weakly convex roof. The outline of ring 2 is more uniformly arched with weak longitudinal grooves. Pleural lobes very strongly convex, terminating vertically.

Plan. Outline longitudinally elliptical. Breadth of axis rather greater than breadth of a pleural lobe. Axial furrows only slightly curved and with rounded but narrow termination.

Twelve rings. The articulating half-ring is narrow and strongly arched, and the articulating furrow deep and narrow. In ring 1 the preannulus is a weak arch less than half length (sag.) of postannulus and without tubercles. The postannulus bears tubercles and is shorter (sag.) than ring 2. The interannular furrow is very weak and only distinct on the crest of the ring. The succeeding rings are even bands which arch forward slightly. The ring furrows are only slightly less deep from the axial furrows to the longitudinal grooves. The latter are weak and situated between the outer pair of tubercles.

Tubercles strong with height at least equal to diameter: rings 1–2 with nine, the median smaller than the others, rings 7–10 with six.

Ten ribs posterior to which are two more, represented by two parallel rows of three to four tubercles posterior to the axis. Rib 1 moderately curved; the remainder only weakly so. Ribs strongly arched with deep pleural furrows; 1–5/6 clearly divided by a prominent rib furrow which terminates well before margin. Anterior portions twice as wide as posterior portions and tubercular 1 with 7, 8 with 4. Posterior portions with small close-set tubercles; 1 with 8/9. Border poorly demarcated and indistinct border furrow. Anterior portions continue prominently to margin but except on ribs 1–2 posterior portions terminate at border furrow.

Development and variation. The smallest pygidium (GS 86986) has ten rings and ribs. It is comparatively broader, has less prominent posterior portions to the ribs, and the preannulus is not developed. A somewhat larger pygidium (GS 86988) has twelve rings and eleven ribs plus one more, shared, at the termination to the axis. The proportions of this specimen are almost the same as those of the holotype. In the Belgian specimen (BR IG 9136) the axis tapers less strongly, the border furrow is more prominent, and the posterior portions of the ribs also are more prominent.

Measurements (in mm.)

	GS 86984 Pl. 43, fig. 17	BR IG 9136 Pl. 43, fig. 20	GS 86988	GS 86986
Length of pygidium	7·8	(8·0)	5·0	2·9
Length of axis	6·7	(7·0)	. .	. .
Breadth of pygidium . . .	(9·0)	9·2	5·6	4·2
Breadth of axis	2·5	3·5	. .	. .

Comparisons. The species differs from *P. salteri* Goldring (1955, p. 42, pl. 2, figs. 8–13) and *P. kassini* (Weber 1937, pp. 48, 128, pl. 9, figs. 42–47) especially in being comparatively longer. It is nearer to the unnamed variety of *P. salteri* (Goldring 1955, p. 43, BU 7987–8) in having anterior portions of the ribs stronger than the posterior portions, and although longitudinal grooves are weakly present there is only one tubercle between the grooves and axial furrows instead of the introduction of a double row. *Metaphillipsia seminifera* (Phillips 1836) has very weak posterior portions to the ribs. The species may be immediately distinguished from species of *Brachymetopus* by the absence of prominent medial tubercles on the axis. In *Phillipsia* Portlock 1843 the posterior portions of the ribs are weakly developed and do not carry tubercles; there is a definite smooth border and no preannulus on ring 1. No preannulus is present in the type species, *P. salteri*, but it would seem that the preannulus is only of specific significance (R. and E. Richter 1956, p. 348).

Occurrence. England, Lower Limestone Shale, Bristol, Avon Gorge: (1) right bank, holotype (above) and pygidia (GS 86985–8); (2) left bank, in 8 ft. shelly limestone occurring 9 ft. 6 in. above top of Bryozoa Bed, pygidium; Shepton Mallet, Windsor Hill Quarry horizon β, ?cranidia (BU 1144, 1148); Belgium (all specimens in BR), Hastière and Étroeungt Beds (Tn1a) Hastière 1, Insemont Road, partially preserved complete specimen (IG 10865) (it is not known how the stratigraphical horizon of this locality differs from the following); Hastière Limestone (Tn1b) Hastière 1, Insemont Road, pygidium (IG 9136); *peracuta*-Shales (Tn2a) Dinant 25, Gendron-Celles, Furfooz road, pygidium (IG 14007), Méverquies, Duchâteau quarry, pygidium (IG 10024/a), Landelies, Limestone Quarry, pygidium (IG 9540a); Landelies Limestone (Tn2b) Feluy 41, abandoned quarry east of Feluy 31, ? pygidium (IG 13829).

Brachymetopus sp.

A single cephalon (GS 86989) was found *in situ* in the Lower Limestone Shale (top of K_1 Subzone), right bank, Avon Gorge, Bristol. Only the anterior border is fully preserved. The border is wide, very slightly convex, and ornamented with a single row of tubercles (4 to 5 per mm.). It is not distinguishable from *Brachymetopus woodwardi* Whidborne 1896 (Goldring 1955, p. 44). *B. maccoyi* (Portlock 1843) seems to have a proportionally wider border.

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A CARBONIFEROUS *SELAGINELLITES* WITH *DENSOSPORITES* MICROSPORES

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Abstract. *Selaginellites canonbiensis* sp. nov., a small lycopod cone compression from the Upper Carboniferous of Scotland, is described and figured. Its megaspores agree with the spore species *Setosisporites hirsutus*, and its microspores are of the *Densosporites* type. Populations of spores of these two types associated in the Shafton Coal, Yorkshire, compare closely with those from the cone. This correlation suggests that *Selaginellites* may have been the dominant component of the vegetation which gave rise to *Densosporites*-rich coals of the durain type

INTRODUCTION

In the last thirty years maceration studies of Palaeozoic rocks, particularly coals, have resulted in the description of several hundred species of isolated spores and pollen. Inevitably, the parent plants (and so the true affinity) of many of these types is unknown. For stratigraphical work this aspect is usually regarded as of secondary importance, and interest has centred on the vertical and horizontal distribution of the various spore types. However, these records of isolated spores have acted as an incentive to closer study of the spores contained in fossil fructifications. As this information accumulates it becomes possible to interpret a Palaeozoic spore assembly in terms of its parent plants, as in the pollen analysis of Quaternary peats.

One of the commonest of Carboniferous 'small spores' of which the parent plant has hitherto been unknown is *Densosporites*. This paper describes an Upper Carboniferous herbaceous lycopod cone which contains spores of this type; its megaspores also prove to be of a type long known isolated from Upper Carboniferous coal macerations. This correlation of *Densosporites* with a herbaceous lycopod has significant ecological implications which are discussed below.

It is a pleasure to be able to express my thanks to Dr. F. W. Anderson, Chief Palaeontologist of the Geological Survey, who has made possible the loan and examination of the holotype from the Kidston Collection. I am also grateful to Professor J. Walton for permission to examine a slide in the Kidston Slide Collection in the University of Glasgow, and to Professor T. M. Harris F.R.S. for helpful advice.

DESCRIPTION OF THE CONE

The lycopod cone described below as *Selaginellites canonbiensis* sp. nov. (Pl. 44, figs. 1–3) is a compression in dark shale from the Byre Burn Group of the Canonbie Coalfield, Dumfriesshire, Scotland. As the exact relationship of this group with the Coal Measures of other areas has not been established, the age of the cone can only be given as Westphalian (Upper Carboniferous). Associated with it on the same piece of shale are *Sphenophyllum cuneifolium* (Sternb.), *Asterophyllites equisetiformis* (Schloth.), *A. sp.* cf. *charaeformis* (Sternb.), and several leafy shoots of the *Lycopodites* type.

The cone compression shows a series of sporangia arranged spirally around an axis which they completely conceal. Projecting beyond each sporangium and appearing to

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come from beneath it is the free end of the sporophyll lamina. This is most easily seen at the side of the cone (Pl. 44, fig. 2), where the lamina can be seen turned parallel to the cone axis. In the living cone these overlapping scale-like distal ends of the sporophylls would have covered and protected the sporangia, as in a typical *Selaginella* cone. The sporangia, as seen in the compression, consist largely of the 'mummified' remains of the spores they contained. The lower sporangia can be seen under a binocular microscope to contain megaspores, as their outlines show clearly through the coalified remains of the sporangial wall. This megaspore-bearing zone is succeeded by one of apparently smooth, uniform sporangia in the apical part of the cone. A fragment removed from this zone and macerated for about twelve hours with Schulze's solution (concentrated nitric acid and potassium chlorate), followed by ammonia solution, yielded hundreds of microspores (Pl. 44, figs. 4–7). These were mounted in glycerine jelly. A number of megaspores were removed from the cone with a needle and treated with Schulze's solution followed by ammonia, to remove adhering coaly matter. Some of these were mounted in air cells as opaque objects for examination by reflected light; the remainder were further treated with Schulze's solution until transparent, washed, and mounted in balsam for examination by transmitted light (Pl. 44, figs. 9 and 10). When using Schulze's solution for clearing spores in this way (as distinct from freeing them of coaly matter) treatment with ammonia was omitted as this not only darkens them but also may corrode the spore wall.

The cone is apparently intact at the apex, but the base is incomplete. The difference in the appearance of the microsporangia and megasporangia makes the transition between the two zones (about half-way up Pl. 44, fig. 2) quite evident. A single megasporangium occurs slightly above this level, but the transition is otherwise abrupt.

Apart from their gross morphology nothing in the way of structure of the sporophylls can be seen, and no cuticle was obtained from the sporophyll lamina.

THE MEGASPORES

The exact number of megaspores in each sporangium is not clear. The one megasporangium occurring among the microsporangia appears to contain only one tetrad; in the zone of megasporangia lower down the cone the outlines of the individual sporangia cannot be clearly discerned, but these, too, probably contained only a single

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EXPLANATION OF PLATE 44

Figs. 1–3 are photographed by reflected light; Figs. 4–11, by transmitted light.

Figs. 1–3. Holotype of *Selaginellites canonbiensis* sp. nov. 1, marked with white pointer, ×1. Photographed under xylol. 2, ×4. Note the *Lycopodites* type shoot to the left of the cone. 3, × 4, photographed dry, with oblique illumination from the bottom right.

Fig. 4. A group of microspores from *S. canonbiensis* sp. nov., ×130.

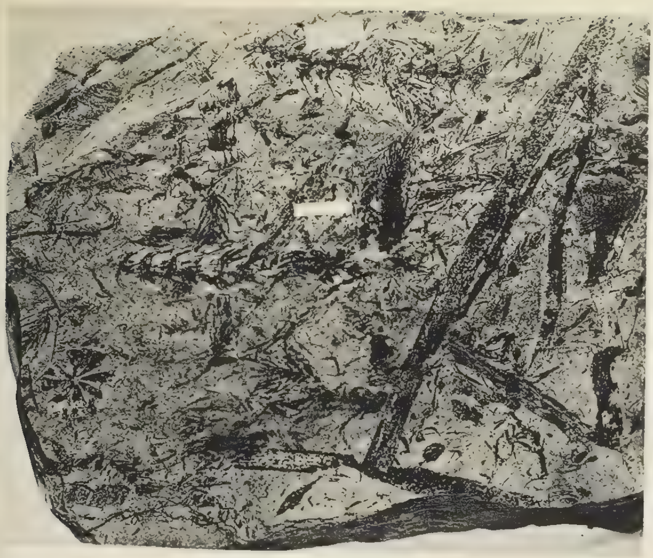
Figs. 5–7. Microspores from *S. canonbiensis* sp. nov., ×500.

Fig. 8. Microspore, *Densosporites sp.* cf. *loricatus* from the Shafton Coal, stained with safranin. ×500.

Figs. 9 and 10. Megaspores from *S. canonbiensis* sp. nov., ×50.

Fig. 11. Megaspore, *Setosisporites hirsutus* from the Shafton Coal, ×50. The spines appearing to be on the contact faces are in fact on the distal face of the spore, and are merely seen through the smooth contact faces.

Location of the specimens: Geological Survey and Museum, London. Figs. 1–3, Kidston Collection 3153. Figs. 4–6, Kid. Coll. 3153A. Fig. 7, Kid. Coll. 3153B. Fig. 8, Mik (C) 277. Fig. 9, Kid. Coll. 3154A. Fig. 10, Kid. Coll. 3154B. Fig. 11, Mik (C) 282.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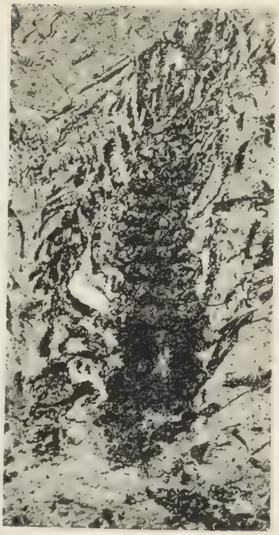
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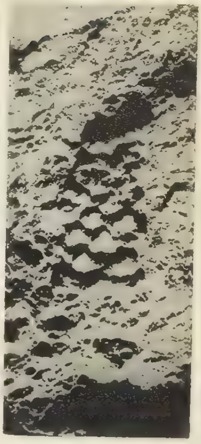
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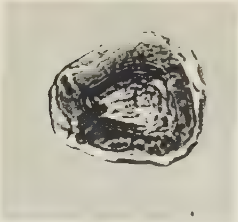
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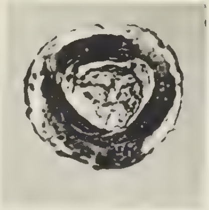
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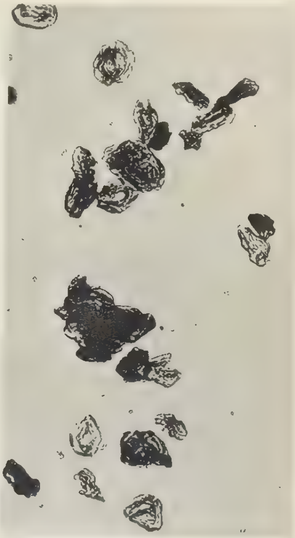
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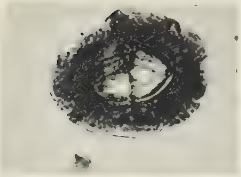
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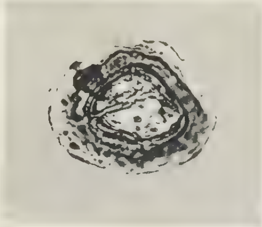
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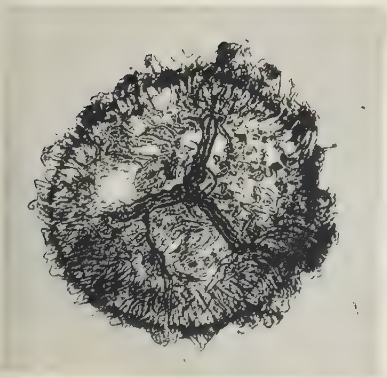
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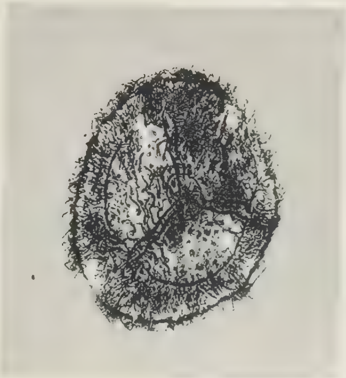
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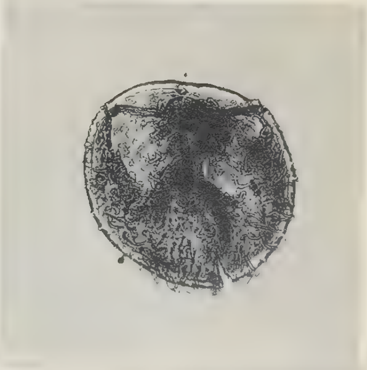
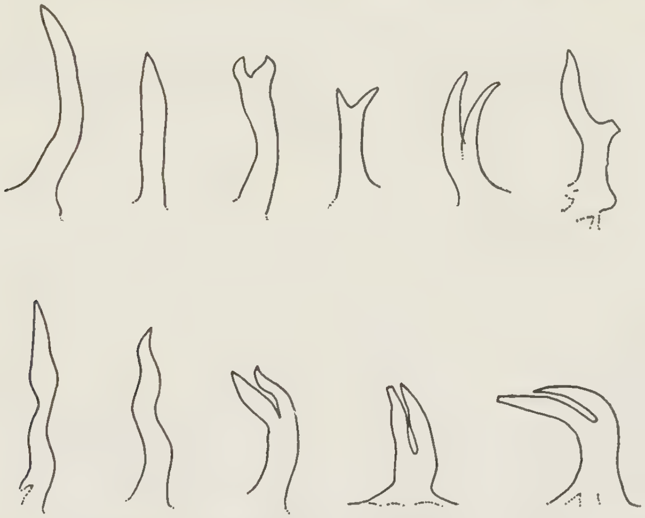

9 x50

tetrad. From the size of the megaspores it is unlikely that there were more than four tetrads per sporangium at most.

The megaspores must originally have been more or less spherical, as the compressed spores have a circular outline regardless of their orientation when compressed (Pl. 44, figs. 9 and 10). They have a clear triradiate marking, and at the centre of the three ridges a small hollow globular prominence is present. The contact faces are smooth, but the remainder of the spore is uniformly covered with spines mostly around $60\,\mu$ long, which may branch once (text-fig. 1). The spines have a slightly expanded trumpet-shaped base, but above this are more or less cylindrical for about two-thirds of their length, tapering in the apical one-third to a sharp point. They may branch at any level, but no more than a single bifurcation was seen. The branched and unbranched spines are mixed haphazardly, with the former in the minority. The triradiate ridges are about five-eighths of the spore radius as seen in specimens squashed in the equatorial plane. They have a fine suture running along their length, but no specimens were seen to have split open along this suture as though germinating. The contact faces are delimited mainly by their being rather thinner than the remainder of the spore wall, and by the abrupt cessation of the spines.

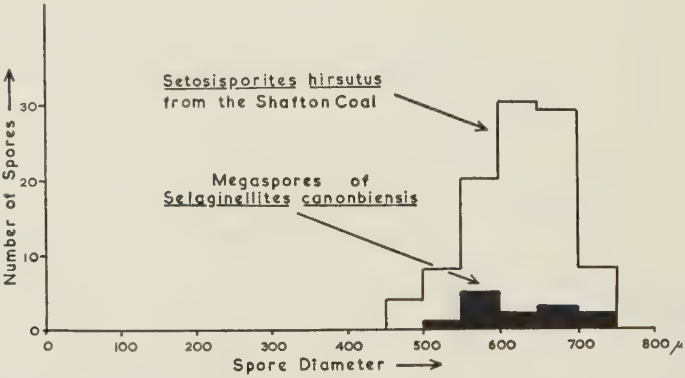


TEXT-FIG. 1. Spines from megaspores of *Selaginellites canonbiensis* sp. nov., ×400, showing variation in the branching. Each row of spines is from a single spore. (Slide 3154B, Kidston Collection, Geological Survey Museum: upper row, spore 5; lower row, spore 7.)

Megaspores similar to those occurring in *Selaginellites canonbiensis* sp. nov. occur commonly in Upper Carboniferous coals and are known as *Setosisporites hirsutus* (Loose) Ibrahim (or *Triletes hirsutus* of Schopf, Wilson, and Bentall 1944, Dijkstra 1946, and others). This type of megaspore is known from Upper Carboniferous coals from Germany, Holland, France, and Turkey (see Dijkstra 1946, Potonié and Kremp 1955 for full discussion of synonyms and range). The author has also obtained it from a number of British Upper Carboniferous coals. In a sample from the Shafton seam near Barnsley, Yorkshire (Westphalian C), this was the most abundant type of megaspore present. A specimen from this source is shown in Pl. 44, fig. 11. A histogram of size variation in 100 megaspores from this seam compared with the smaller number extracted from *Selaginellites canonbiensis* sp. nov. is shown in text-fig. 2. The isolated *Setosisporites hirsutus* from the Shafton seam show a rather larger proportion of branched to unbranched hairs, and have less sharply defined contact faces than the megaspores of *Selaginellites canonbiensis* sp. nov.; despite this, the megaspores in the cone, if found isolated, would be correctly included in *Setosisporites hirsutus*.

THE MICROSPORES

On maceration the contents of the microsporangia disintegrated almost completely into individual spores (Pl. 44, figs. 4–7, text-fig. 4A and B), leaving some clusters and occasionally individual tetrads still adhering together. A number of preparations were made, representing several hundred microspores; all were of essentially the same type, and no obviously different (i.e. foreign, contaminating) spores were seen. A histogram based on two measurements (inner diameter of the spore, and overall diameter) of each of 100 spores is shown in the lower half of text-fig. 3. This is at least consistent with the hypothesis that the spores represent a single population, namely the original contents of the cone. The spores range from 36–53 μ diameter with a mean of 43 μ.



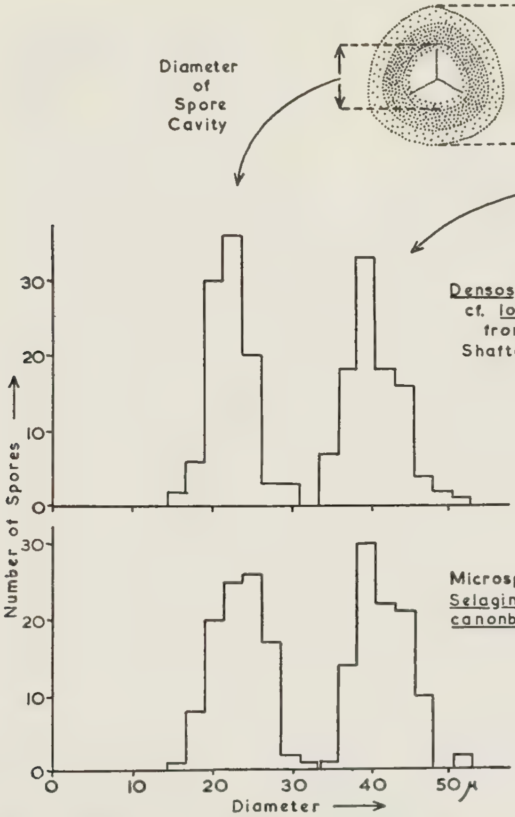
TEXT-FIG. 2. Histograms showing the similarity of size distribution in *Setosisporites hirsutus* from the Shafton Coal, Yorkshire, and megaspores extracted from *Selaginellites canonbiensis* sp. nov. The largest dimension of the spore was measured in each specimen. Based on 100 of the isolated spores and 13 from the cone. (Slides nos. Mik (C) 278–81 incl.; Kidston Collection nos. 3154A and B, 3153D, Geological Survey and Museum, London.)

The spores were originally oblate, with a round to subtriangular equatorial outline. The equatorial zone of the spore was apparently greatly thickened so as to form a rim (the *cingulum* of Potonié and Kremp) diminishing in thickness towards the periphery. The proximal and distal faces of the spore were evidently very thin and are often torn or missing. The triradiate marking is sometimes evident as three sutures or slits in the proximal face which extend only as far as the inner edge of the cingulum (text fig. 4).

Spores similar to the microspores of *Selaginellites canonbiensis* sp. nov. are a common constituent of Carboniferous coals, and have been assigned to the spore genus

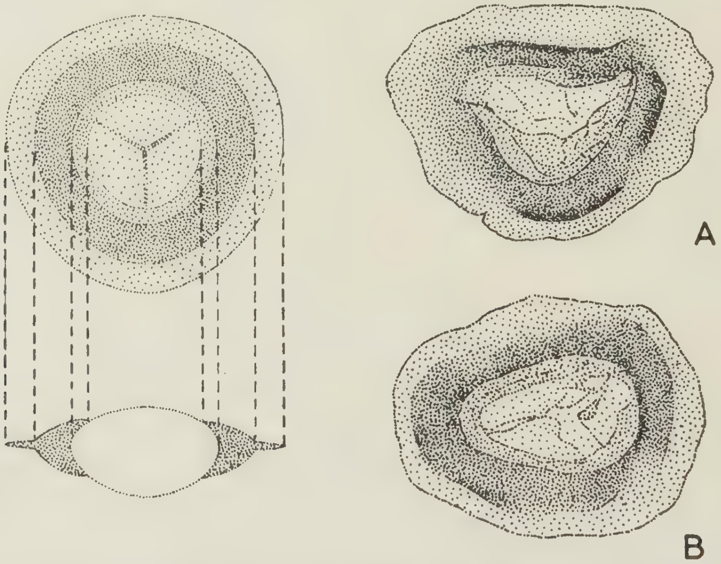
Densosporites. Of the Upper Carboniferous species cited by Potonié and Kremp (1956*a*) the spores in the cone show best agreement with *D. loricatus* (Loose) S.W. and B.

The sample of the Shafton Coal which contained abundant megaspores agreeing with those in *Selaginellites canonbiensis* sp. nov. was also examined for small spores. A species of *Densosporites* similar to *D. loricatus* was found to be more abundant than any other single spore type present. One of these spores from the Shafton Coal is shown in Pl. 44, fig. 8 (the optical density of the spore in this photograph is exaggerated by its being stained with safranin). The demarcation between the inner (darker) zone of the cingulum and the outer (lighter) zone is not so marked as in the microspores from the cone, but otherwise they show good agreement. A histogram based on 100 spores from this coal is shown above that of the microspores from *Selaginellites canonbiensis* sp. nov. in text-fig. 3.



TEXT-FIG. 3. Histograms showing the similarity of size distribution in populations of *Densosporites sp.* cf. *loricatus* from the Shafton Coal, and microspores from *Selaginellites canonbiensis*. Each population gives two sets of measurements; the inner diameter of the spore cavity, and the overall diameter. Based on 100 spores of each population. (Slide nos. Mik (C) 276; Kidston Collection 3153A and B, Geological Survey and Museum, London.)

It seems reasonable to suppose that these isolated small spores (*Densosporites sp.* cf. *loricatus*) and the larger *Setosisporites hirsutus* occurring together in the Shafton Coal were produced by a single species of parent plant which was closely similar to *Selaginellites canonbiensis* sp. nov. It does not follow that all Upper Carboniferous spores assigned to the genera *Setosisporites* and *Densosporites* represent the megaspores and microspores respectively of *Selaginellites*; but this is probably so for at least some other species of the three genera concerned.



TEXT-FIG. 4. A and B, two microspores from *Selaginellites canonbiensis* sp. nov., ×1,000, showing the thicker and thinner parts of the cingulum. C, a diagrammatic reconstruction at the same scale, showing the unflattened spore in plan and polar section (with the proximal face uppermost). (A and B from slide 3153C, Kidston Collection, Geological Survey and Museum, London.)

TAXONOMIC POSITION OF THE CONE

The genus *Selaginellites* was first described by Zeiller (1906). His species (*S. suissei*) was based on a number of specimens which were similar to typical *Selaginella* species in two important respects. Firstly, they were heterosporous, with *Selaginella*-like terminal cones; and secondly, the leafy shoots were heterophyllous (a character of many, but not all, living Selaginellas). Zeiller (1906), Halle (1908), and Seward (1910) have recommended that *Selaginellites* should be reserved for those fossil *Selaginella*-like forms known to be heterosporous. Subsequently two petrified Carboniferous *Selaginella*-like cones have been described: one of these (Darrah 1938) was actually placed in the genus *Selaginella*; the other (Hoskins and Abbott 1956) in *Selaginellites*. Although nothing is known of the vegetative structure in these cases, the attachment of the sporangia and the presence of a ligule are additional features of agreement with *Selaginella*. Finally, Lundblad (1948) has assigned to *Selaginellites* a small heterosporous lycopod cone compression. This constitutes a reasonable extension of the use of *Selaginellites* to include a small detached heterosporous cone lacking direct evidence as to its vegetative parts.

The detached cone described here is in the same category as Lundblad's cone in that no direct evidence as to the nature of its parent plant is available. The cone is associated with some fine leafy shoots but the identification of these with *Lycopodites*, *Selaginellites*, *Bothrodendron*, &c., is questionable (cf. Zeiller 1888, pp. 486–96; Němejc 1947, pp. 72–73; Chaloner 1953, pp. 286–7). The general morphology of the cone is *Selaginella*-like; it is far smaller than typical *Lepidostrobus*, and indeed is smaller than several species of *Selaginellites*. The evidence for the affinity of *S. canonbiensis* sp. nov. is to this extent exactly comparable with that on which Lundblad assigned her Triassic cone to *Selaginellites*. This involves a broad interpretation of the genus, and must be subject to any new evidence as to the vegetative character of the parent plant.

COMPARISON WITH *POROSTROBUS* NATHORST

Nathorst (1894) described a small cone (5·5 mm. diameter) from the Lower Carboniferous of Spitzbergen as *Lepidostrobus zeilleri*. Later (1914), he suggested that it should be placed in a separate genus for which he proposed the name *Porostrobus* on the basis of its association with *Porodendron*, although he acknowledged that the connexion with that genus had not actually been demonstrated. In his later paper, Nathorst (1914, pl. 5, figs. 15 and 16) illustrated microspores obtained from this cone by maceration, and from his figures these spores are evidently similar to *Densosporites*. Examination of a slide prepared by Nathorst in the Kidston Slide Collection (Glasgow University) confirms this. Although the microspores are rather poorly preserved they evidently possessed a greatly thickened cingulum. Nathorst was unable to make a clear preparation of the megaspores, which were about 500 μ in diameter.

All that is known of Nathorst's specimen is that it is a small heterosporous lycopod cone detached from its parent plant. On this basis a case could be made for placing it in *Selaginellites*, rather than its being made the holotype of a distinct genus. Its main significance in this context is in its showing a further correlation of an undoubted species of *Densosporites* with another small lycopod cone similar to *S. canonbiensis*.

COMPARISON WITH A CONE ATTRIBUTED TO *BOTHRODENDRON*

Watson (1908) attributes a small petrified megaspore-bearing cone to *Bothrodendron mundum* on the basis of stelar anatomy and other more indirect evidence. The megaspores in this cone show some similarity with those in *Selaginellites canonbiensis* sp. nov. but the hairs on them are much longer, and are restricted to the equatorial zone, where they form a broad fringe around the spore. In this respect they differ also from the isolated megaspores *Setosisporites hirsutus*. As this is the type species of *Setosisporites*, it seems unwise to base a correlation of this spore genus with *Bothrodendron* (cf. Potonié and Kremp 1956*b*, p. 72) on the evidence of Watson's cone.

The megaspore structure is the only feature on which detailed comparison between *S. canonbiensis* and Watson's cone may be made, owing to their different modes of preservation. For the reasons cited above, this comparison indicates that the cones are at least specifically distinct.

ECOLOGY OF *SELAGINELLITES CANONBIENSIS* SP. NOV.

A number of spore workers have remarked on the frequent association of *Densosporites* with so-called splint-coals (e.g. Schopf *et al.* 1944, p. 40). Kremp (1952) and Smith

(1957) have recently discussed the possible ecological significance of this. Kremp considers the Carboniferous coal-forming vegetation to have been of two main types, 'forest moor' and 'open moor'. The first gave rise mainly to vitrite and clarite and the latter to durite. Smith has plotted the distribution of various types of microspores through the thickness of several Carboniferous coal seams, and obtained 'spore spectra' analogous to those obtained from Quaternary peats. A general pattern of orderly progression emerges, and he concludes that this 'suggests strongly that during the formation of certain seams there was a progressive change in the coal swamp environment which was marked by the occurrence of three major floral communities'. These were characterized by the dominance of the three spore types *Lycospora*, *Densosporites*, and *Laevigatosporites*, the latter being prominent in a transition phase between the two former. He concludes that *Densosporites* appears 'to be derived from vegetation growing in association with the deposit subsequently to become durite'.

It has already been shown (Schopf *et al.* 1944; Chaloner 1953; Felix 1954) that *Lepidodendron* and possibly *Lepidophloios* produced spores of the *Lycospora* type. These arborescent lycopods must have been the main source of spores in Smith's *Lycospora* phase and indeed may have been the dominant plants of Kremp's forest moor. The microspores present in *Selaginellites canonbiensis* sp. nov. now suggest that Smith's *Densosporites* phase represents an abundance of herbaceous lycopods, and that these were probably the main component of Kremp's open moor vegetation.

SYSTEMATIC DESCRIPTION

Selaginellites canonbiensis sp. nov.

Plate 44, figs. 1–7, 9–10

Diagnosis. Small lycopod cone, at least 15 mm. long and 3·5 mm. wide. Sporangia in the axils of spirally arranged sporophylls, of which the distal portion ascends for about 2·5 mm. Sporangia seen in surface view about 0·75 mm. wide. Microsporangia in the apical region, megasporangia below. Megaspores originally more or less spherical, with triradiate symmetry, 530–710 μ diameter, mean of thirteen specimens 630 μ. Triradiate ridges about five-eighths the spore radius in length, 20–30 μ in height and width, with a small (120 μ diameter) hollow prominence at the spore apex. Contact faces smooth; remainder of the spore covered with spines of more or less uniform length (about 60 μ), some of which branch once. Spines slightly swollen at the base tapering gradually in the lower two-thirds and then more rapidly to a sharp point. Spore wall uniform in optical section 25–30 μ thick. Microspores originally oblate, round to subtriangular in equatorial outline, with triradiate marking often faint or obscure; diameter 36–53 μ, mean of 100 specimens, 43 μ. Equatorial region of spore greatly thickened to form a cingulum diminishing in thickness towards the periphery. Wall very thin in the polar areas. Inner diameter of spore cavity 17–34 μ, mean of 100 specimens 25 μ.

Isolated megaspores agreeing with those in this cone have been assigned to *Setosisporites hirsutus* (Loose) Ibrahim; isolated microspores agreeing with those in the cone have been included in the genus *Densosporites* (cf. *D. loricatus*).

Holotype. Nos. 3153 and 3154, Kidston Collection, Geological Survey and Museum, London.

Locality and Horizon. The holotype is from the left bank of the River Eck, about 30 yards below the junction with Byre Burn, Canonbie, Dumfriesshire, Scotland, and was collected in 1902. This horizon is between the Three-Quarter Coal and the Main Coal of the Byre Burn Group (Westphalian), see Barrett, Richey, and Graham (1945).

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ALGAL DEBRIS-FACIES IN THE CRETACEOUS OF THE MIDDLE EAST

by GRAHAM F. ELLIOTT

Abstract. A rock-type common in the Lower and Middle Cretaceous of the Middle East consists of fine algal debris in a calcareous marly matrix. The algae, of which *Permocalculus* and *Munieria* are the commonest, are described and illustrated both as fragments and as complete segments; the origin of the deposits is discussed by analogy with present-day algal sediments.

INTRODUCTION

A CHARACTERISTIC rock-facies in the Cretaceous of the Middle East is that of fine-grained limy marls and marly limestones containing numerous fragments of calcareous algae: in thin section these rocks show the algal fragments as white against a grey background. This 'debris-facies' is known from Iraq, Oman, and the Hadhramaut: the component algal genera are known variously from Europe and North Africa, and the facies probably has a wide Tethyan distribution. In the Middle East it occurs locally at various Lower and Middle Cretaceous levels, but is particularly characteristic of the Barremian-Aptian horizon.

The algae are sometimes accompanied by foraminifera, and occasionally by other organisms, and there is a varying proportion of non-algal debris, but it is the algal fragments which are the distinctive features of the rock: so much so, that particular types of fragments were used for stratigraphic purposes before they were definitely recognized and referred to genera and species. Much of this debris is too small for the particles to be individually recognizable: identification has therefore depended upon rare fortunate preservation of larger pieces, patient comparison of all fragments with theoretically-possible sections of suspected identification-species, and such illustrations of fragments in thin-section as exist in the general literature.

This paper is based on investigations carried out for Iraq Petroleum Company, Ltd., and is published by permission of the Chief Geologist and Management of that company.

THE FLORA

The genera represented are few in number; they are most commonly *Permocalculus* and *Munieria*, secondarily *Actinoporella*, *Clypeina*, and *Salpingoporella*, and more rarely *Triploporella* and one or two dasyclads and codiacids not yet determined. Acicularian spicules are not uncommon: these are naturally dissociated after the death of the plant, and behave similarly during sedimentation to the mechanically broken fragments of the other genera.

Permocalculus (Pl. 45, 47, 48) is represented by at least two species: the common *P. inopinatus* (Elliott 1956) in the Barremian-Aptian, and a new species from the Albian-Cenomanian, described below. Other species are not yet fully known. The genus, which ranges from the Permian, has many points in common with the modern *Galaxaura* (Pl. 46, figs. 1, 2), a segmented chaetangiacid alga which is an inhabitant of warm shallow

[Palaeontology, Vol. 1, Part 3, pp. 254–9, pls. 45–48.]

littoral waters in the Pacific, West Indies, and elsewhere: the relationship has been discussed elsewhere in detail (Elliott 1955*a*, 1956), but it seems likely that this kind of plant has always grown in much the same environment. Cretaceous *Permocalculus* are known also from France and North Africa. In the Middle East innumerable fragments of segments are common, and are recognizable by the denticulated edge occasioned by pores in the calcified crust: single complete segments, and two or more attached segments, are very rare.

Munieria baconica Deecke was described from the Hungarian Lower Cretaceous (Deecke 1883), and subsequently recorded by Taeger (1936) from the Aptian of this area. A reconstruction attempted by Pia (1920) shows the alga to have a thin main stem with well-spaced horizontal whorls or verticils of about twelve or fourteen relatively coarse straight primary branches. Both stem and verticils are coated with calcareous matter, the latter very thickly, so that around the stem they are fused into coarse ring-like structures. Carozzi (1948) recorded this species from the Swiss Purbeckian, giving a valuable set of figures of thin-sections of debris. His material seems to be of a larger form having a proportionally wider central stem-canal than that of the type, and about sixteen primary branches per whorl. The Middle East material comes from the same approximate horizon as the type-material, as dated by foraminifera and other fossils, but it shows the characters of the older, Swiss, material, and is identified by reference to Carozzi's text-figures.

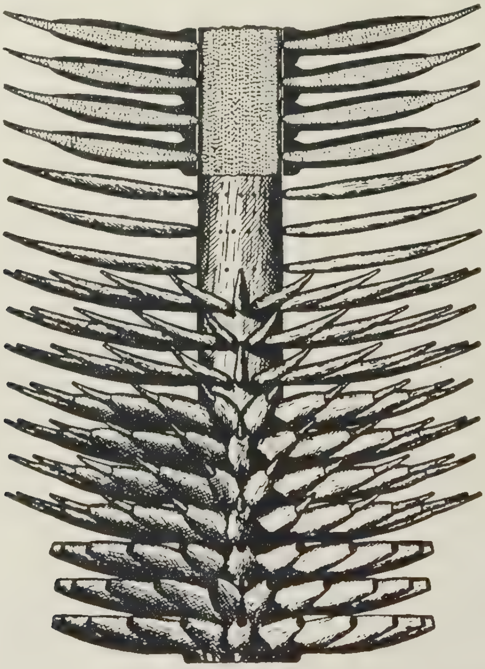
Munieria is the most fragmentary alga of all in the debris-facies (Pl. 45, fig. 4), and most of the finer fragments, associated with recognizable *Munieria*-crumbs are intrinsically quite indeterminable. The coarser fragments show in thin-section as little hooked and looped scraps. Such as have been recognized have been correlated with Carozzi's Swiss specimens determined by him as *M. baconia*, and this applies also to the very rare sections of complete whorls (Pl. 48, fig. 1). It is especially characteristic of the Barremian-Aptian, though met with rarely in the older Cretaceous, and it extends up also into the Albian.

Actinoporella was described from the Polish Portlandian (Alth 1878, 1882), and *A. podolica* (Alth) has been recorded from the Swiss Purbeckian (Carozzi 1948) and the north Iraq Valanginian-Hauterivian (Elliott 1955*b*, and Pl. 47, fig. 5 of this paper). Somewhat similar in general plan to *Munieria* (see Pia's restoration reproduced here in text-fig. 1) but differing in proportions and number of primary branches to a whorl, the calcareous skeleton is more delicate. Curiously, in spite of this, it seems to have been less fragile, and the fossil remains in the debris-facies are less fragmentary (Pl. 45, fig. 1), often showing in section as chains of connected rings. Possibly the calcareous coating was less porous than in *Munieria*.

Of the minor elements in the debris-flora, *Clypeina*, long known from Jurassic and Tertiary, has now been recorded from many levels in the Cretaceous (Emberger 1957); it is uncommon so far as known in the Middle East Cretaceous. *Salpingoporella* is represented by occasional remains (Pl. 46, fig. 3) comparable with the type *S. mühlbergi* (Lorenz), known from the Barremian-Aptian of Switzerland and France. Dissociated acicularian spicules (Pl. 45, fig. 2), some identified as *Acicularia* cf. *antiqua* Pia, a Cretaceous species, are not uncommon. Such spicules are the skeletal remains of the terminal disks of *Acicularia*, a genus still surviving and somewhat like the more familiar Recent *Acetabularia* or 'Mermaids' wineglass', a shallow warm-water genus.

CONDITIONS OF ACCUMULATION

Living algae comparable to those listed above are all littoral or lagoonal inhabitants of warm, very shallow waters, and it is reasonable to suppose that the Cretaceous flora grew under similar conditions. The rocks in which their fragmentary remains occur,



TEXT-FIG. 1. *Actinoporella podolica* (Alth), from the Upper Jurassic of Poland, as reconstructed by Pia (1920): ×20 approx.

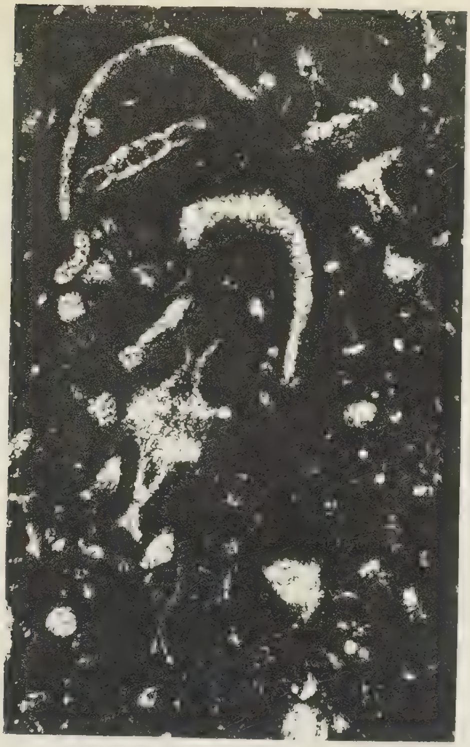
EXPLANATION OF PLATE 45

Thin-sections in the collections of the Geological Department, Iraq Petroleum Co., Ltd., London.

1. Debris-facies, showing *Actinoporella podolica* (Alth), × 28. Valanginian-Hauterivian of Banik, Mosul Liwa, northern Iraq; reg. no. Wl. 11539.
2. Debris-facies, showing *Acicularia sp.*, × 55. Barremian of Sarmord, Sulemania Liwa, north-eastern Iraq; reg. no. Wl. 10381.
3. Debris-facies; *Permocalculus inopinatus* Elliott and *Orbitolina sp.*, × 15. Aptian of Koi Sanjak, Erbil Liwa, north-eastern Iraq; reg. no. DM. 539.
4. Debris-facies; fine debris including '*Munieria baconica* Deecke', × 15. Aptian-Albian of Surdash, Sulemania Liwa, north-eastern Iraq; reg. no. Wl. 10396.

EXPLANATION OF PLATE 46

1. *Galaxaura cylindrica* (Sol.) Kjellm. Portion of growth × 2, to show calcified segments as they occur during life. Recent; Boston Beach, Portland Parish, Jamaica, B.W.I.
2. *Galaxaura sp.* Flattened segments × 5, to illustrate paired growth of segments in this type of alga. Recent; West Indies.
3. Debris-facies, showing *Salpingoporella* cf. *annulata* (Lorenz), × 30. Valanginian-Hauterivian of Jebel Gara, Mosul Liwa, northern Iraq; reg. no. Wl. 6380, in the Geological Department, Iraq Petroleum Co., Ltd., London.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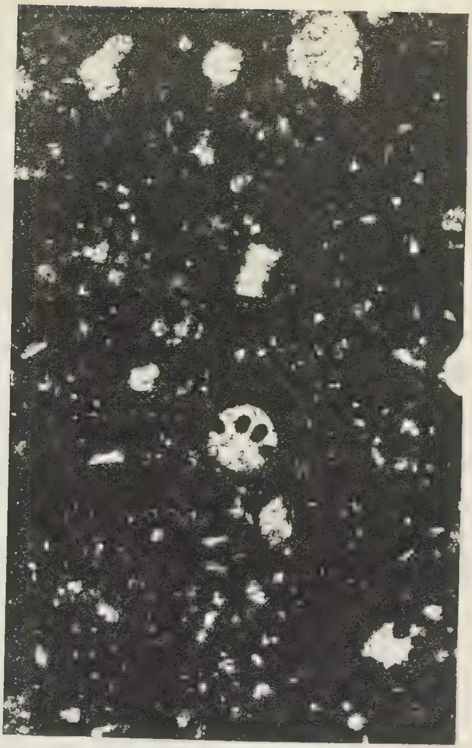
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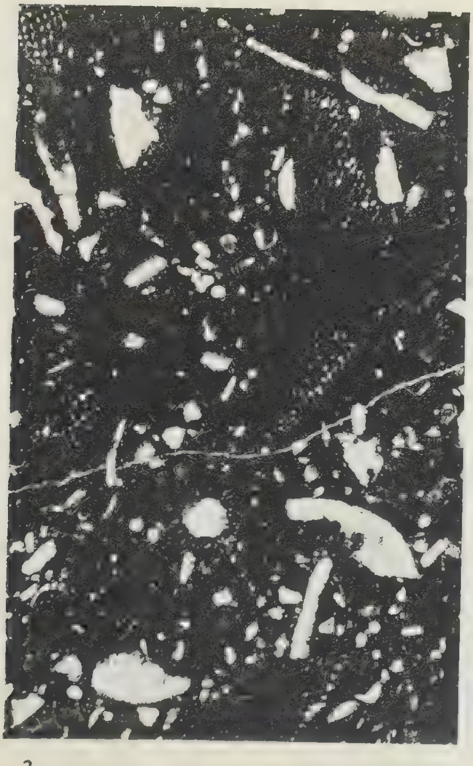
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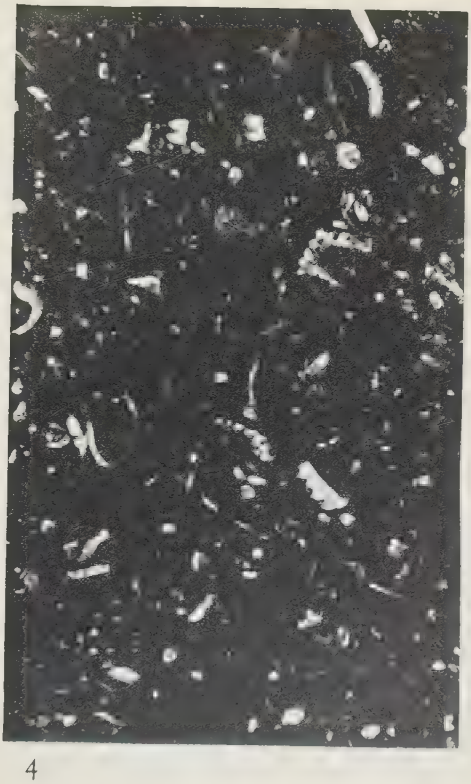
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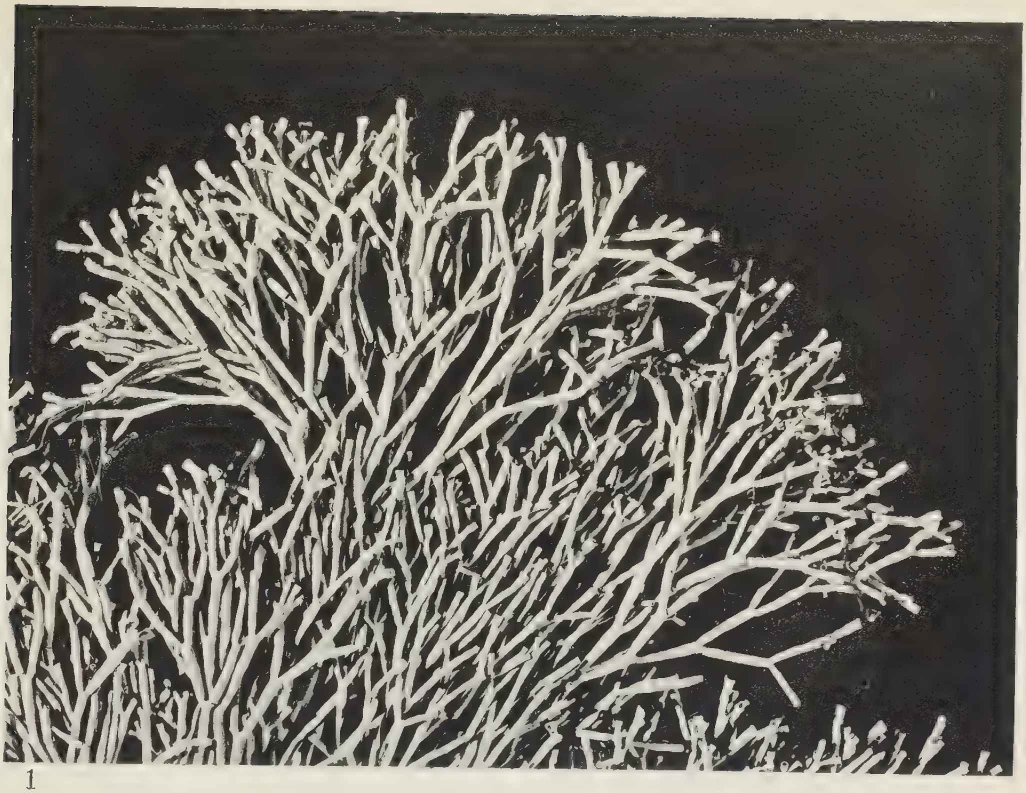
ELLIOTT, Cretaceous algae



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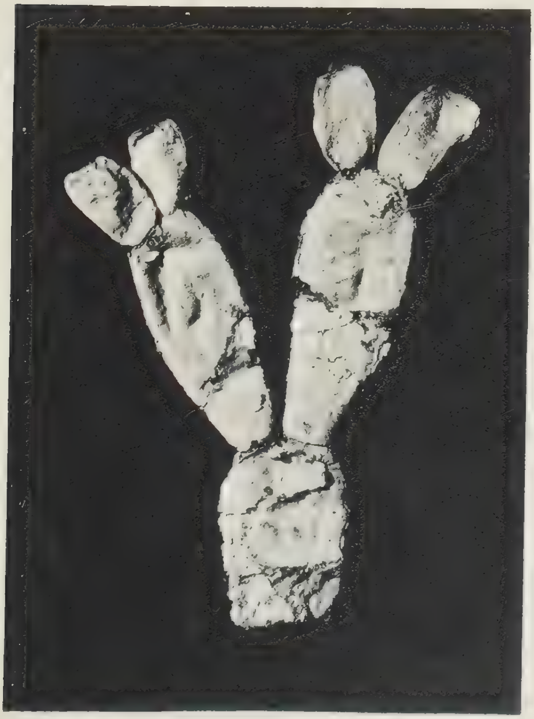

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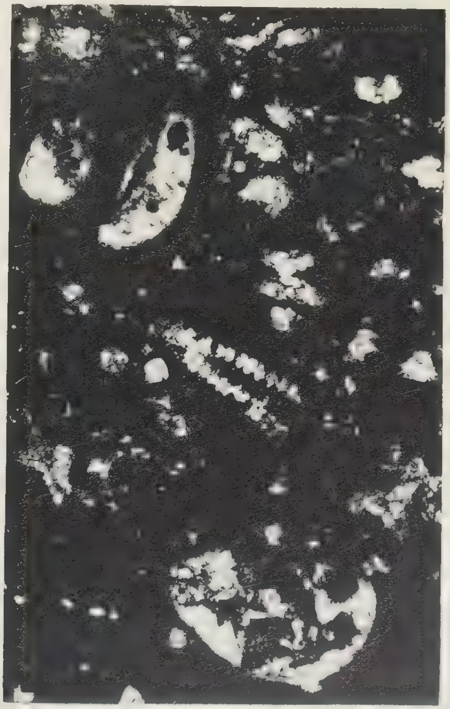

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ELLIOTT, Recent and Cretaceous algae

however, are old fine-grained sediments, often with no other fossils but small foraminifera, whatever depth of water is tentatively assigned for their accumulation.

Examination of the extensive literature on Recent marine deposits is helpful, but does not give an exact analogy. *Halimeda*, a modern warm-water green calcareous alga of the type under consideration, is the cause of extensive deposits of calcareous segments, whole and broken, within atoll lagoons in the Indo-Pacific (cf. Chapman and Mawson 1906). The rock thus formed is analogous with fossil deposits showing an identifiable profusion of calcareous algae associated with remains of numerous shallow-water invertebrates, and is very different from the debris-facies. Outside the reefs a common algal deposit is a mechanically-produced lime-sand formed mostly of debris from the reef-building red algae, though *Halimeda*-material may be present as a minority constituent. Other largely algal deposits are the fine calcareous flour produced as a digestion-product by the parrot-fishes and their allies, which browse on coral and algal reefs, as early noted by Darwin and others, and a sediment of microscopic dissociated aragonite-needles from various green algae (Lowenstam 1955). None of these are comparable to the debris-facies.

From the reports of the U.S. project at Bikini (Emery, Tracey, and Ladd 1954) the following details were gleaned as to the occurrence of *Halimeda*-remains outside the reefs, on the steep outer atoll-slope, which at certain points descends to 1,500 fathoms in 4 miles and 2,000 fathoms in 7 miles. At 80 fathoms there occurred a sediment with whole unbroken *Halimeda*-segments and large foraminifera of up to 12 mm. diameter, both having slipped down from above. At 240 fathoms coarse *Halimeda*-debris (pieces of 6 mm. diameter) was a constituent, while at 410 fathoms there was fine *Halimeda*-debris, of 1 mm. maximum diameter and mostly much less. True *Globigerina*-ooze was found at 1,000 fathoms depth. Although the Cretaceous debris varies from medium-sized algal fragments associated with the larger foraminifer *Orbitolina* to fine fragments without *Orbitolina*, no exact analogy is possible between the Recent calcareous 'slope-sediments' and the Cretaceous 'debris-facies', and it would seem that the latter is a product of conditions existing in the Middle East in Cretaceous times, which are not now well developed.

Three such conditions seem necessary and are in accord with other evidence. They are, firstly, abundance of a warm-water littoral flora of small, separate-growing calcareous algae, like members of the modern families codiaceae, dasycladaceae, and chaetangiaceae, and the absence of extensive growths of the more massive crusting, nodular, and reef-forming algae, included in the family corallinaceae. These latter are in fact rare in the Lower Cretaceous, achieve local abundance in the Upper, and only occur commonly and in profusion in the Tertiary and at the present day.

Secondly, extensive post-mortem fragmentation and dissociation of the calcareous algal skeletons is necessary. These skeletons are fragile tubes and units, with very many pores and sporangial and other cavities: they are known to break down naturally at the present day into sediment-constituents of various sizes which are subject to normal marine transport.

Finally, the existence of a shelf-sea of shallow to moderate water-depth seems called for: this was the normal inter-orogenic Mesozoic pattern, rather than the sharper post-glacial features of the present day. During sedimentation, fine calcareous mud particles were accompanied by the relatively larger algal fragments of lower specific gravity: the presence or absence of *Orbitolina* may indicate different depths, but nothing comparable to the submarine slopes at Bikini.

Thus the debris-facies may be regarded as indirect witness to both topographical and biological conditions during the Cretaceous, in that portion of the Tethyan Ocean which now, upheaved and desiccated, forms the Middle East.

DESCRIPTION

Permocalculus irenae sp. nov.

Plate 47, fig. 2; Plate 48, figs. 2–6

Description. Thallus segmented, formed of units or segments about 2·3 mm. long by 0·75–1·0 mm. wide, each segment giving rise to two segments distally, the latter occasionally preserved as small terminal growths, indicating fossilization of growing segments. Segments approximately circular in cross-section: calcification variable between a thin peripheral zone and a nearly solid segment: sporangia internal, subcortical, often numerous but ill defined, apparently ovoid, one example measuring 0·100 by 0·175 mm. Pores clearly visible at the outer edge of the calcification, where they are fine and irregularly curved.

Holotype. The specimen figured in Pl. 48, fig. 2 from the subsurface Cenomanian of Mileh Tharthar Well, Dulaim Liwa, northern Iraq. Iraq Petroleum Company, Ltd., Geological Dept. Coll., reg. no. MT. 356A.

Paratypes. The specimens figured in Pl. 48, figs. 3, 4, 5, from the same locality and horizon, reg. nos. MT. 356A, B, MT. 360.

Other material. Numerous specimens from the same locality and horizon; also known from about the same horizon, Zubair Wells, Basra, south Iraq; also a specimen from the Albian of Surdash, Sulemania Liwa, north-eastern Iraq.

EXPLANATION OF PLATE 47

1. Typical pores of *Permocalculus inopinatus* Elliott, tangential cut, × 100. Aptian of Jebel Gara, Mosul Liwa, northern Iraq; reg. no. Wl. 6405.
2. Typical pores of *Permocalculus irenae* sp. nov., tangential cut, × 100. Subsurface Cenomanian of Mileh Tharthar Well, Dulaim Liwa, northern Iraq; reg. no. MT. 358.

3, 4. Longitudinal and transverse sections of segments of *P. inopinatus*, × 30. Aptian of Ru Kuchuk, Chama, Mosul Liwa, northern Iraq; reg. nos. DM. 1286, 1284.

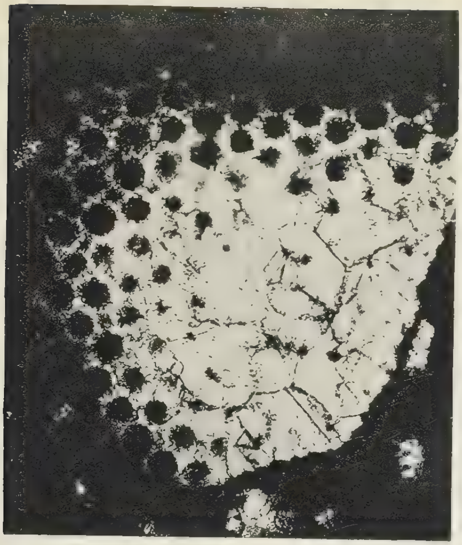
5. Horizontal section through a verticil of *Actinoporella podolica* (Alth), × 60. Valanginian-Hauterivian of Jebel Gara, Mosul Liwa, northern Iraq; reg. no. Wl. 6379.

EXPLANATION OF PLATE 48

Thin-sections in the collection of the Geological Department, Iraq Petroleum Co., Ltd., London.

1. Horizontal section through a verticil of '*Munieria baconica* Deecke', × 50. Aptian-Albian of Surdash, Sulemania Liwa, north-eastern Iraq; reg. no. Wl. 10418.

2–6. *Permocalculus irenae* sp. nov. Subsurface Cenomanian of Mileh Tharthar Well, Dulaim Liwa, Iraq; reg. nos. MT. 356A, B; MT. 360. All × 28. 2, Near-vertical section, holotype. 3, Segments in association: 4, Transverse section: 5, Longitudinal section; all paratypes. 6, Typical coarse debris.



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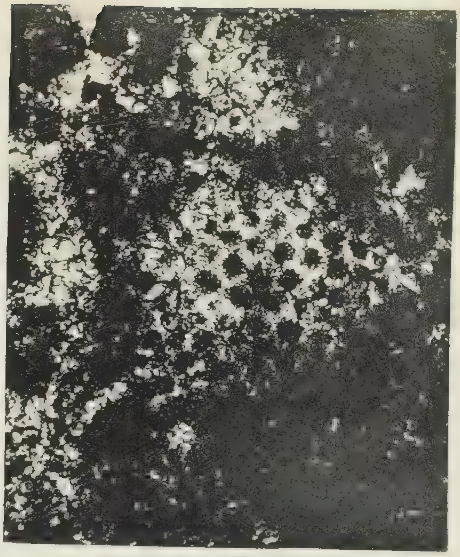

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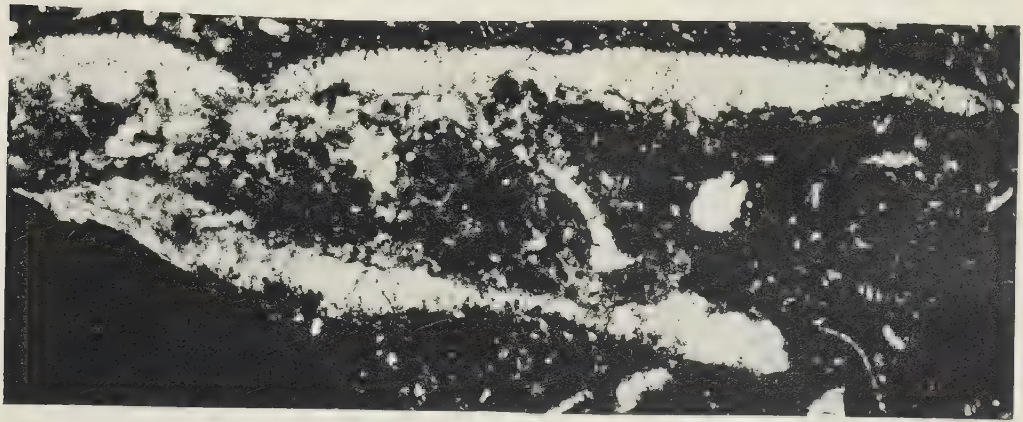

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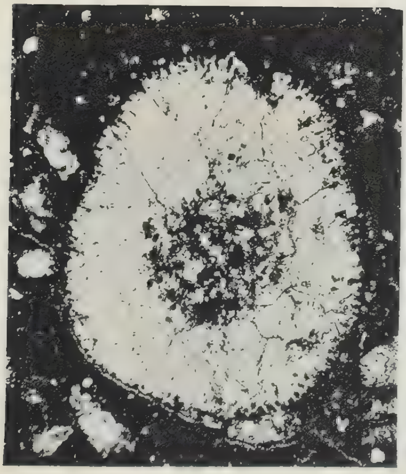

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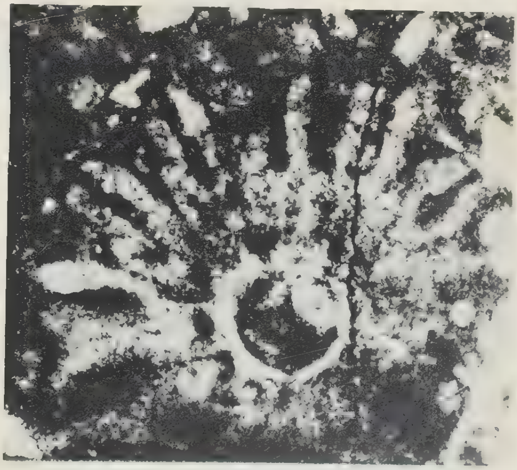

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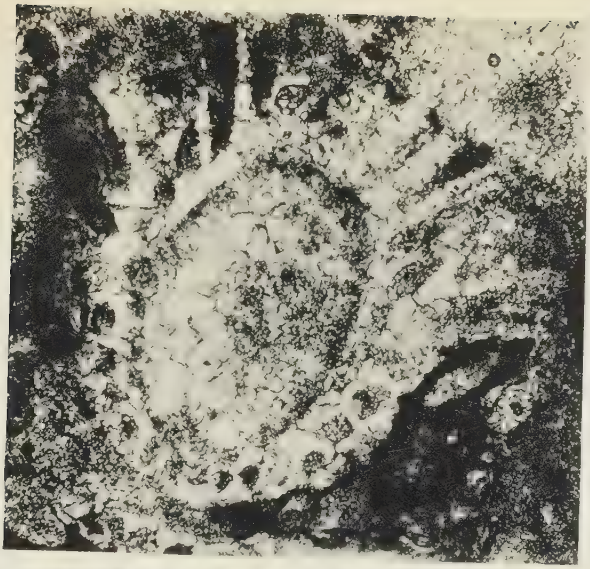
ELLIOTT, Cretaceous algae



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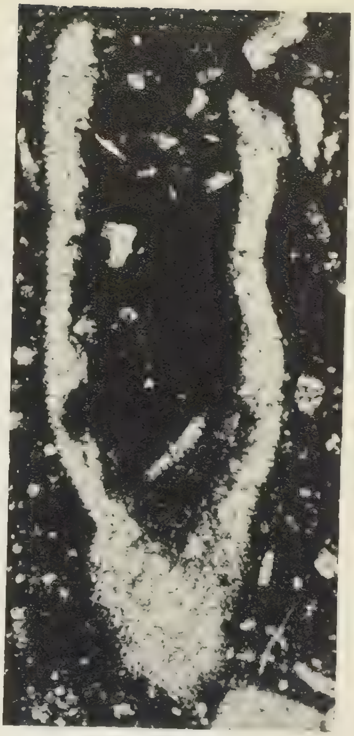

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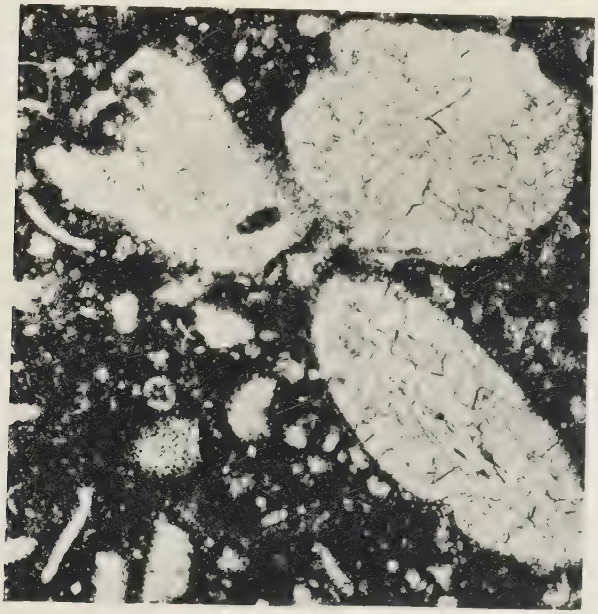

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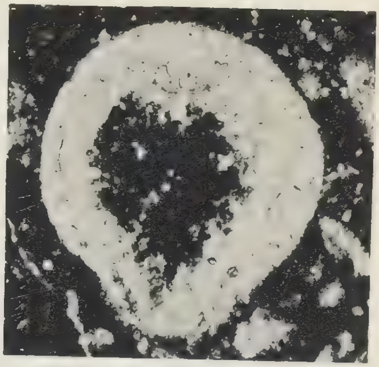

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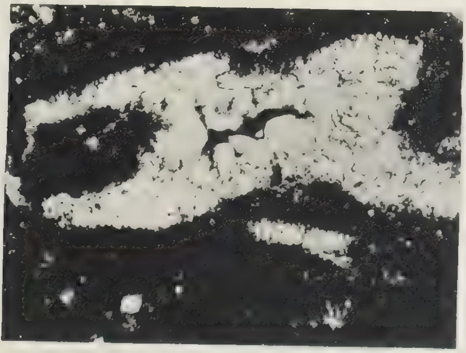

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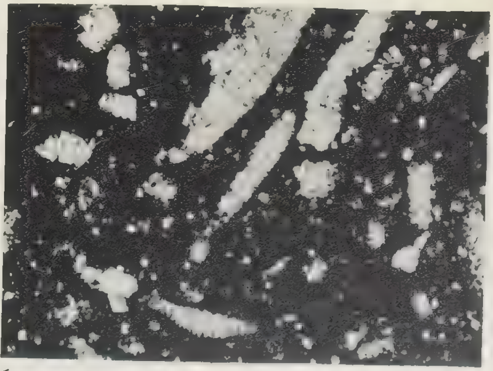

6

ELLIOTT, Cretaceous algae

Remarks. Permocalculus irenae is very similar to the older *P. inopinatus* Elliott (Pl. 47, figs. 1, 3, 4) from the Barremian-Aptian, and may be regarded as its descendant. The distinguishing features are pore-diameter, condition of common occurrence, and segment-size. In *P. inopinatus* the diameter of the pores where they widen at the surface to notch the profile in section is usually about 0·020 mm. (occasionally up to 0·030 mm.): in heavily-calcified stem segments they may be only 0·010 mm. or less, but these specimens are a minority. In *P. irenae* they are all about 0·010 mm. (observed limits 0·007–0·015 mm.). *P. inopinatus* usually occurs as fine debris, almost comminuted, with complete or near-complete segments very rare: *P. irenae* is fragmentary but not comminuted, and complete and associated segments are not uncommon. When found, such segments are smaller in *P. irenae* than in *P. inopinatus*, where they may attain dimensions of 5·0 by 1·75 mm.

This species is dedicated to Mrs. Irene Barber, to whom the writer is indebted for the typing of most of his papers for the last decade.

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